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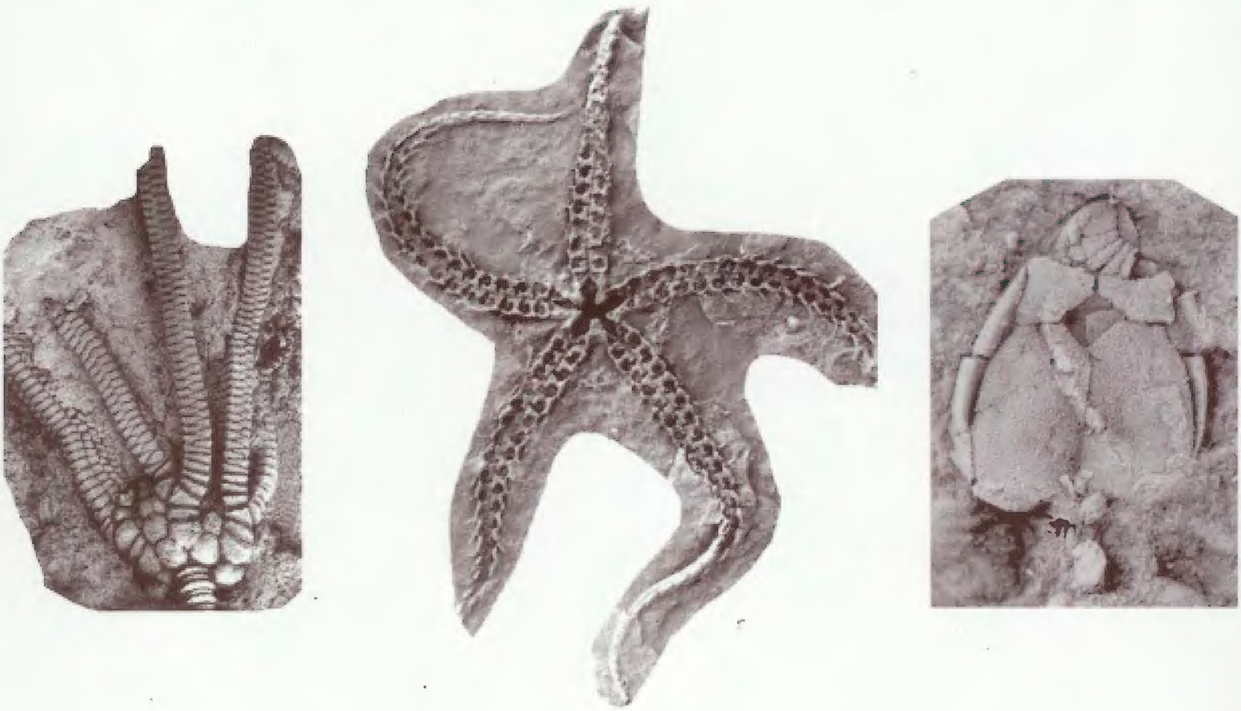

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# SILURIAN AND DEVONIAN CRINOIDS FROM CENTRAL VICTORIA

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Crinoids have long been known from middle Palaeozoic clastics in central Victoria but this is the first comprehensive attempt to document the fauna; 54 taxa are described; 25 are camerates (ca), 7 disparids (d), 19 cladids (cl) and 3 flexibles (f). New taxa are the genera *Hollowaycrinus calvus* (ca), *Duncanicrinus calvariolus* (ca), *Frankocrinus holmesi*, *F. enidae* (ca), Pterinocrinidae gen. nov. (ca), *Darragherinus tomi* (d), *Kroppocrinus heathcotensis*, *K. mathiesonensis* (d), *Stewbrecrinus terryi* (cl), *Holmesocrinus enidae*, *H. idaensis* (cl) and *Quadritaxocrinus websteri* (f); camerate species *Ophiocrinus muettae*, *Dimerocrinites bispinosa*, *Eucrinus clarkae*, *Eudimerocrinus ekardti*, *E. gilli*, *Nexocrinus wallanensis*, *Hexacrinites chirnsidensis*, *Oehlerticrinus lemenni*, *O. jeani*, *Alisocrinus lineatus*, *Clematocrinus perforatus* and *C. argylensis*; disparid species *Trichocrinus morleyi* and *Phimocrinus hanschi*; cladid species *Codiacrinus secundus*, *Cupulocrinus austrogracilis*, *Dendrocrinus arrugius*, *Plicodendrocrinus australis*, *Shintocrinus cometensis*, *S. richi*, *Antihomocrinus chapmani*, *Nassoviocrinus corcorani*, *Dictenocrinus ibaeypus* and *D. remotus*; and the flexible *Meristocrinus quatriramus*. ❒ *Crinoids, Silurian, Devonian, Victoria.*

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Middle Palaeozoic sequences in the Melbourne Trough of central Victoria have yielded rich fossil faunas since the middle of last century but the diverse crinoid component has been largely ignored among echinoderm groups (Withers & Keble, 1934a and b; Jell, 1983). Possibly the first record and certainly the first illustration of crinoids from central Victoria was that of Blandowski (1855) but he figured only stem columnals and did not follow with the descriptive paper promised. Bather (1897) first described an articulated crinoid, *Hapalocrinus victoriae*, with a line drawing that he acknowledged in a footnote as being somewhat uncertain. Photographs of Bather's (1897) specimen and its counterpart (Bather claimed it was lost) are provided below and show that the cup is poorly known. Chapman (1903) described *Helicocrinus plumosus* and *Botryocrinus longibrachiatus* from the Silurian of the Melbourne area. Both are reviewed below with the latter re-assigned to *Nassoviocrinus* Jaekel, 1918.

More recent reports of crinoids in clastic sequences of central Victoria are restricted to : 1, Talent (1965:17, pl. 4, fig. 2) noted crinoid stem ossicles as a common element throughout the Heathcote sequence and crowns at localities 41 (=*Hapalocrinites argylensis* sp. nov., below) and 42 from where he figured the unidentifiable external mould of a crown; 2, *Crotalocrinites* from Heathcote (Jell, 1982) and; 3, *Kooptoonocrinus nutti*, *Codiacrinus rarus*, *Dendrocrinus saundersi* and a new genus of Dimerocrinitidae (=*Duncanicrinus calvariolus* below) from near the Silurian/Devonian boundary east of Melbourne (Jell in Jell & Holloway, 1983). Numerous other records of crinoids in these sequences (e.g. Williams, 1964; Gill & Caster, 1960) simply noted them among wider faunal listings without naming or describing taxa. Other described crinoids from Victoria occur in limestones at Lilydale (Bates, 1972), Mansfield (Jell et al., 1988) and Toongabbie (Philip, 1961). In the rest of Australia, Devonian crinoids have been described from limestones in Queensland and NSW (Jell et al., 1988) and *Pisocrinus* (referred to *Parapisocrinus* by Rozhnov, 1981) and *Lecanocrinus* have been reported from the Silurian at Yass (Etheridge, 1904; Chapman, 1934).

## BIOSTRATIGRAPHY

The sections from which these crinoids have been collected span the Ludlow and Pridoli of the Silurian and the Lochkov of the Devonian. However, soil cover, urban development and metamorphism around intrusions limit available sections. Virtually all the echinoderms known have been collected from quarries, road cuttings, creek beds or other man-made exposure.

| Wenlock | Ludlow | | | | Prid-oli | Lochkov | | | | | | Pragian |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Aegiria thomasi* | | | *Not. Plentiensis* | | *Boucotia janeae* | | | *Boucotia australis* | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | |
| *Dendrocrinus* sp. | X | O | O | | O | | | | | | | *Trichocrinus morleyi* |
| *Dendrocrinus arrugius* | | X | X | X | | | | | X | | O | *Hollowaycrinus calvus* |
| *Nassoviocrinus corcorani* | | X | X | | | | | | O | | O | *Ctenocrinus signatus* |
| *Hapalocrinus victoriae* | | X | | | | | | | O | O | O | *Ctenocrinus paucidactylus* |
| *Helicocrinus plumosus* | | X | | | | | | | O | | | *Dimerocrinites bispinosus* |
| *Nassovio- longibrachiatus* | | X | | | | | | | O | | | *Eucrinus clarkae* |
| *Phimocrinus americanus* | | X | | | | | | | | | X | |
| *Clematocrinus argylensis* | | X | | O | | | | | O | | | *Clematocrinus perforatus* |
| *Alisocrinus lineatus* | | | | X | | | | | | | O | *Frankocrinus holmesi* |
| *Phimocrinus hanschi* | | | | X | | | | | O | | | *Frankocrinus enidae* |
| *Shintocrinus cometensis* | | | | X | O | | | | O | | O | *Duncanicrinus calvariolus* |
| *Antihomocrinus chapmani* | | | | X | | | X | | X | | X | |
| *Quadritaxocrinus websteri* | | | | X | | | | | O | | | *Nexocrinus* sp. |
| *Holmesocrinus enidae* | | | | | X | | | | O | | | *Plicodendro- australis* |
| *Nexocrinus wallanensis* | | | | | X | | | | | | O | *Stewbrecrinus terryi* |
| *Kroppo- heathcotensis* | | X | | | | | | | O | | X | *Codiacrinus secundus* |
| *Cupulo- austrogracilis* | | | | | | X | | | | O | | *Holmesocrinus idaensis* |
| *Hexacrinites chirnsidensis* | | | | | | | X | | O | | | *Darraghcrinus tomi* |
| *Ophiocrinus nnettae* | | | | | | | | X | | | O | *Kroppo- mathiesonensis* |
| *Eudimerocrinus gilli* | | | | | | | | X | | | O | *Meristocrinus quatriramus* |
| *Ctenocrinus stellifer* | | | | | | | X | X | X | | O | *Decacrinus* sp. |
| *Dictenocrinus remotus* | | | | | | | | X | | | O | *Ancyrocrinus* sp. |
| *Dictenocrinus ibaeypus* | | | | | | | | | X | O | | *Crotalocrinites pulcher* |
| *Kooptoonocrinus nutti* | | | | | X | | | | O | | O | *Eudimerocrinus eckardti* |
| *Geroldicrinus* sp. | | | | | | | | X | O | | O | *Oehlerticrinus lemenni* |
| *Shintocrinus richi* | | | | | | | | X | O | | O | *Oehlerticrinus jeani* |
| Pterinocrinidae gen. nov. | | | | | | | | X | | | O | Myelodactylid indet. |
| *Dendrocrinus saundersi* | | | | | X | | | | | | | |
| *Codiacrinus rarus* | | | | | X | | | | | | | |

FIG. 1. Distribution of crinoids in the Silurian-Devonian clastic sequences of central Victoria; all species listed are dealt with in this paper, Jell & Holloway (1983) or Jell (1982). The international scale is correlated to the local Brachiopod Assemblage Zone scheme of Garratt (1983) in the top two rows, following Garratt & Wright (1988). The numbering sequence of columns in the third row refers to aggregates of localities as listed in the Appendix; detailed relative levels of widely distributed localities is uncertain and these must be seen in many cases as best approximations. Occurrence of taxa listed on the left of the figure are indicated with 'X' and those on the right by 'O'. Generic names ending in a hyphen require addition of the suffix *crinus* and are shortened to fit a single line.

Structure within the Melbourne Trough consists of tight folding with long approximately N-S axes, also limiting measurable sections. Fossils occur in profusion in a few horizons; they are relatively rare in many other horizons; but most of the sedimentary sequence is unfossiliferous. Brachiopods are the most common group among the shelly fauna and have been used to establish a preliminary biozonation (Fig. 1) against which the shelly faunas have been placed in sequence (Garratt, 1983). The crinoids described herein come mainly from the few horizons where fossils are prolific and preservation is superb; very large numbers of articulated echinoderms occur there. For example, NMVPL252 provides the greatest diversity of crinoids and of echinoderms in the Melbourne Trough. This locality was originally a small road metal quarry but most available

material came from a new excavation of the quarry in the summers of 1980-1983 undertaken by the author with the sustained help of Frank and Enid Holmes and Steve Eckardt and occasional help of several others. Those localities that yield only one or 2 species mostly represent localities where fossils are rare and their age determined by stratigraphic position. The crinoid localities (Appendix) are placed in approximate relative stratigraphic sequence (Fig. 1) using these best available data. The brachiopod zonation of Garratt is related to the international stage scale with graptolites that occur at a few horizons through the sequence (Garratt & Wright, 1988).

The crinoids described herein are not significantly useful biostratigraphically as they occur relatively rarely in terms of both localities and horizons. Nevertheless there are clear differences between the Ludlow and Lochkov faunas for example and the continued study of this fossil group with other elements of the shelly fauna will continue to refine what is at present a very preliminary brachiopod zonation.

## PALAEOECOLOGY

Palaeoecological settings in the Melbourne Trough were discussed in a number of papers (Garratt, 1983; Cas, 1983; Vandenberg & Wilkinson, 1982; Vandenberg, 1988, 1992). Cas (1983, fig. 17) provided a schematic diagram of regional palaeogeography for SE Australia showing the Melbourne Trough as a long narrow embayment of the ocean with ample neighbouring relief and continued subsidence to provide the thick pile of clastic sediments. Localities rich in articulated echinoderms occur in distal turbidites (PL252) or extensive thin sand units (within a finer grained sequence) (PL300, 229, 1924). Both these settings indicate catastrophic events causing the death and fast burial of these animals (Jell, 1983) but the cause or causes of such events remain unclear.

## PALAEOBIOGEOGRAPHY

These crinoid faunas provide few useful data for palaeobiogeographic reconstruction as they contain taxa otherwise restricted to North America or to Europe and other taxa common to both those areas. Few other parts of the world have well enough described crinoid faunas of this age for meaningful comparison. At the generic level there are slightly more representatives of the European fauna as is the case with brachiopods (Boucot et al., 1969) but among camerates there are more American affinities.

## SYSTEMATIC PALAEONTOLOGY

Material described is housed in the Museum of Victoria (NMVP) and the localities are registered in the same Museum (NMVPL). Specimens are preserved in decalcified clastics so are found in the form of internal and external moulds often partially infilled with iron oxides making the mould less than faithfull. Morphological detail of the moulds improves with diminishing grain size of the matrix. All illustrations are of latex casts taken from these moulds and whitened with a sublimate of ammonium chloride. Terminology follows Moore & Teichert (1978). Measurements are given as: length, parallel to the central axis; width, transverse to, but never cutting or meeting the central axis; and depth, normal to, and may join the central axis.

Class CRINOIDEA Miller, 1821
Subclass CAMERATA
Wachsmuth & Springer, 1885
Order DIPLOBATHRIDA
Moore & Laudon, 1943
Suborder EUDIPLOBATHRINA Ubaghs, 1953
Superfamily RHODOCRINITOIDEA
Roemer, 1855
Family OPSIOCRINIDAE Kier, 1952

Frest & Strimple (1981) and Ausich (1986a) recognised the close similarity of *Opsiocrinus* Kier, 1952 and *Ophiocrinus* Salter, 1856 and assigned them both to this family; they are considered synonymous by Jell & Theron, 1999. Ausich (1986a) also erected 2 new genera from the Llandovery of Ohio in this family and discussed the group in detail. Inclusion of the Australian *Hollowaycrinus* nov. is discussed under that heading below. This addition necessitates widening the family concept to include a form with radials in lateral contact; this difference has been sufficient to separate taxa at superfamily level in the past (Ubaghs, 1978b). To take an even more heretical view I question whether *Stelidiocrinus* Angelin, 1878 from the Upper Silurian of Gotland should not be included in this family. It has been classified in the Monobathrida because it lacks the second circlet of plates below the radials but it (particularly *S. laevis* Angelin, 1878 as figured by Ubaghs (1978b, fig. 307, 1e)) resembles the Opsiocrinidae very much in cup shape, median column of anal plates in CD interray, 10 biserial arms, few slightly depressed interradial plates and presence of an intersecundibrach. Its first primibrach is shorter and wider than in most Opsiocrinidae but is comparable with that of *O.*

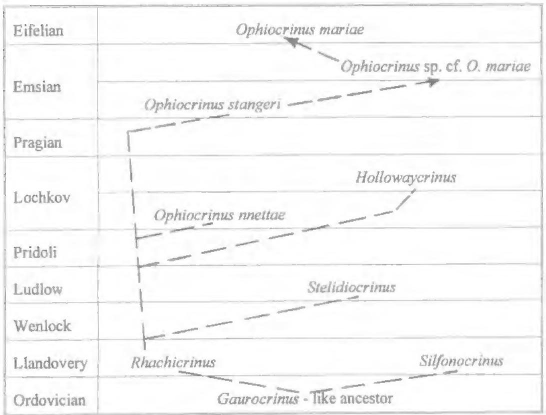



FIG. 2. Sketch of phylogeny of the Opsiocrinidae following Ausich (1986a) and discussion herein.

*nnettae* described below. Throughout the Opsiocrinidae the infrabasals are concealed by the stem attachment and *Opsiocrinus* itself was originally described as monocyclic; I suggest therefore, that a careful examination of the Swedish material of *Stelidiocrinus* should be made to determine this feature. *Stelidiocrinus* would join *Hollowaycrinus* as the second Opsiocrinidae with radials in lateral contact. Witzke & Strimple (1981) suggested that evolution from rhodocrinitid to dimerocrinitid stage (i.e. withdrawl of the first interbrachial to allow lateral contact of radials) occurred several times. They postulated 3 separate occasions from different *Ptychocrinus* stocks so my suggestion of 2 further occasions above is in line with their thinking.

Current knowledge of this family suggests that only small sections of the lineages involved are known (Fig. 2) and I agree with Witzke & Strimple (1981) that a great deal more basic data about Silurian forms in particular will be necessary to refine our understanding.

## **Ophiocrinus** Salter, 1856

TYPE SPECIES. *Ophiocrinus stangeri* Salter, 1856 from the Lower Devonian Bokkeveld Series, South Africa.

REMARKS. This genus is discussed in detail elsewhere (Jell & Theron, 1999). Its occurrence in the Lower Devonian of Victoria in close proximity geographically and temporally with *Hollowaycrinus* gen. nov. makes it quite feasible that one gave rise to the other as remarked under that genus below.

## **Ophiocrinus nnettae** sp. nov.
(Fig. 3)

ETYMOLOGY. An anagram from Annette.

MATERIAL. NMVP149344 from NMVPL1990.

DIAGNOSIS Interrays narrow; primanal in posterior interray contacting C and D radials and 1st primibrachs, supporting 3 anal plates distally; central column of larger hexagonal plates in anal sac. Arms 10, with triangular axillary 2nd primibrach, distinctly biserial above distal to secundibrach. Stem circular, with small but distinct marginal projections on nodals and internodals.

DESCRIPTION. Crown >40mm long, >4 times as long as wide at cup, with arms spreading gently (tips not preserved). Cup low conical, approximately 5mm long, wider than long; plates smooth, convex so sutural margins depressed. Infrabasals presumably concealed by stem. Basals longer than radials, hexagonal, longer than wide. Radials pentagonal, wider than long, separated from each adjoining radial by basals and 1st interprimibrach, with distinctly margined outer ledge across distal margin matched by similar ledge on 1st primibrach, similar matching ledges on succeeding interplate sutures along the arm gradually diminishing in distinctness and size; 1st primibrach rectangular, as wide as radial, short; 2nd primibrach axillary, triangular, as wide as 1st primibrach. Arms 10, subquadrate in section, with flattened outer face; each ray with 2 main rami, uniserial as far as 6th secundibrach, becoming biserial abuptly (3rd in one arm observed) distally, with long pinnule of 5 or 6 pinnulars on each free brachial; only primibrachs fixed in cup; interprimibrachs small and few; 1st largest, contacting basal, 2 radials and 1st primibrachs, supporting 2 long narrow plates distally. Primanal hexagonal though contacting 8 plates, almost as large as basals but not quite as long, supporting 3 anals distally; anal plates numerous, decreasing in size distally, with average size larger than that of interbrachials, distinct central column of decreasing hexagonal plates. Stem circular in section, heteromorphic with slightly different sized (length and diameter) columnals alternating, noditaxis N1, with epifacet on each columnal having an outer circlet of small but distinct tubercles or pseudocirri.

REMARKS. This Victorian species differs from the South African genotype (Jell & Theron,

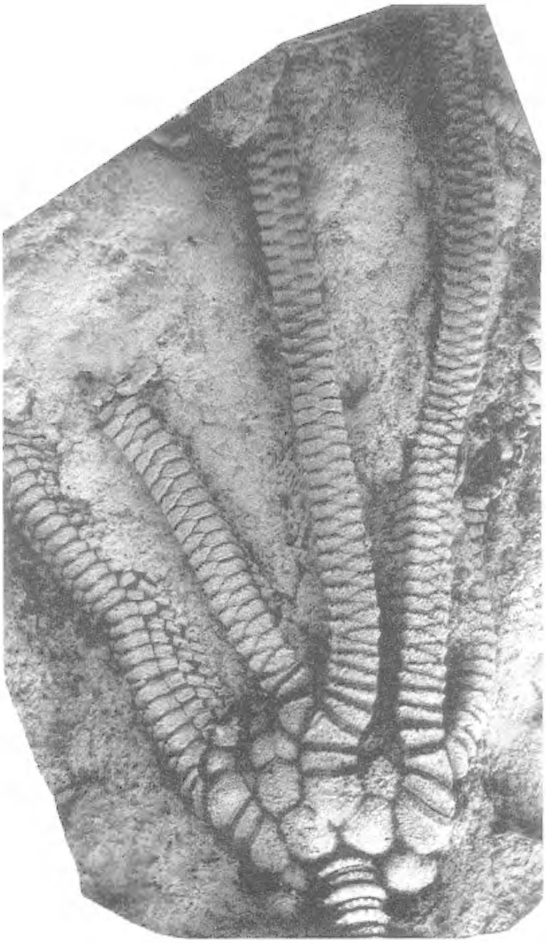


FIG. 3. *Ophiocrinus nnettae* sp. nov., incomplete holotype crown in C ray view, NMVP149344 from NMVPL1990, ×3.

1999) in having fewer interprimibrachs, no intersecundibrachs, distinct ledges on each plate on each interplate suture from radials up to about 3rd secundibrach, its arms becoming biserial much earlier (secundibrach 3 in some arms) and in the stem with tubercles on internodals. From the North American *O. mariae* Kier, 1952 and *O. benderi* (Kesling, 1968), if those are separate species as suggested by Frest & Strimple (1981) contrary to Kesling & Chilman (1975), the Victorian species is distinguished by the same features as separate the genotype as well as a lack of ornament on the interprimibrachs and very short 1st primibrach.

**Hollowaycrinus** gen. nov.

TYPE SPECIES. *Hollowaycrinus calvus* sp. nov.

ETYMOLOGY. For David Holloway who greatly assisted with fieldwork, curation and scientific advice.

DIAGNOSIS. Infrabasals 5, concealed by stem attachment. Radials large, heptagonal, in contact with each other laterally except across CD interray; 1st primibrach hexagonal; 2nd primibrach axillary. Primanal in radial circlet, supporting 3 plates distally, with median column of larger anal plates involving 4 and probably more plates. Arms 10-20, with each ray having 2 main arms becoming biserial distal to the 6th or 8th secundibrach, with some arms branching irregularly once or twice distal to primaxil even though other rami in the same individual are unbranched.

REMARKS. This genus is placed in the Opsiocrinidae based on the similarities in cup shape, 5 concealed infrabasals, median column of anal plates in CD interray, primanal supporting 3 plates, large 1st interprimibrach supporting 2 plates followed by large number of very small irregular plates, 10-20 arms, uniserial to biserial. Conventional classification following Ubaghs (1978) would place this species in *Dimerocrinites* because of the radials being in lateral contact. However, the arms being uniserial proximally then becoming cuneate and finally biserial, the interradial plates being many small ones above a few large ones and the radials being barely in lateral contact all point to an origin from the Opsiocrinidae and it is classified accordingly.

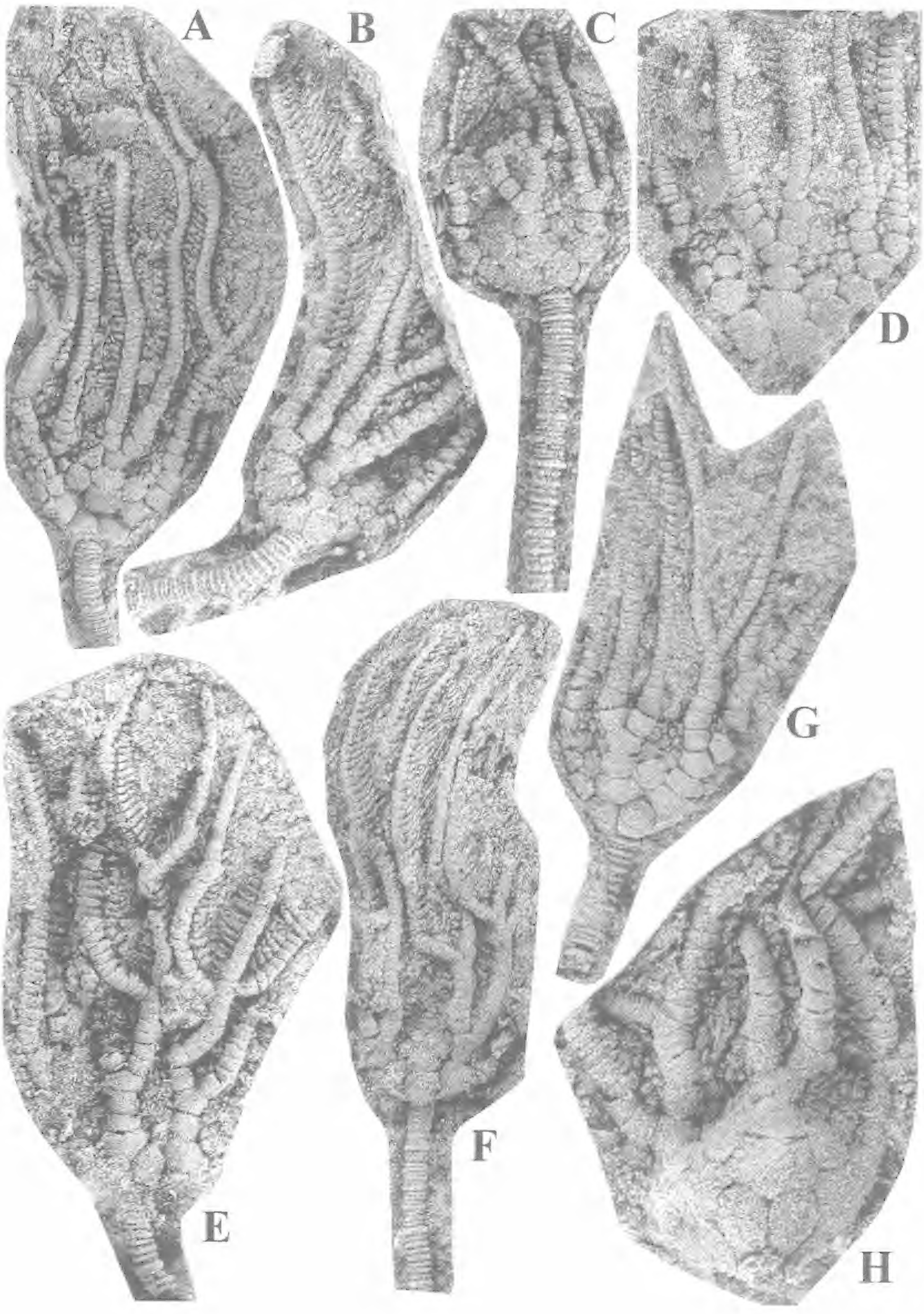
**Hollowaycrinus calvus** sp. nov.
(Fig. 4)

ETYMOLOGY. Latin *calvus*, bald; referring to the lack of median ray ridges and ornament.

MATERIAL. HOLOTYPE: NMVP100158. PARATYPES: NMVP100150, 100153, 107099-107104, all from NMVPL229.

DIAGNOSIS. As for genus.

DESCRIPTION. Crown subcylindrical, averaging 30mm long, at least 4 times as long as wide. Cup low to medium conical, 2-6mm long, just wider than long, of unornamented plates. Infrabasals 5, concealed by stem. Basals 5, longer than radials, hexagonal except for heptagonal posterior one, longer than wide. Radials heptagonal, wider than long, with longer sides contacting basals and 1st primibrach, with short sides contacting adjoining radials or primanal in CD interray; 1st primibrach hexagonal, not as wide as radial and little more than half as long;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2nd primibrach axillary, pentagonal, as wide as 1st primibrach; each ray with 2 main arms, some without further branching, others with 1 or 2 further branchings irregularly, uniserial as far as 6th or 8th secundibrach, becoming biserial distally, with long pinnule of 5-6 pinnulars on each free brachial; arms free distal to 2nd secundibrach; interprimibrachs numerous, with large heptagonal proximal one supporting 3 plates in a row distally, with size decreasing rapidly distally, with distal medial plates depressed. Primanal hexagonal, almost as large as basals, supporting 3 anals; anal plates numerous, decreasing distally, with average size larger than interprimibrachs. Stem circular in section, with slightly different sized (length and diameter) nodals and internodals alternating proximally but distally with noditaxis N212, may be long (no complete stem known but an incomplete one in excess of 9cm known), distal termination unknown. All plates smooth, without ornament.

REMARKS. This species is distinguished from *Ophiocrinus* by most radials just making lateral contact and by variable arm branching. Its separation from dimerocrinitids is discussed above. The arms are highly variable in their branching pattern and also in the arrangement of brachials. Most observable rays divide once and have only 2 arms whereas others may have one undivided arm from the first branching while the second may divide twice more. Most subsequent divisions appear to be at fairly high and variable angles to growth direction; there is a question of whether these could represent a regrowth response to breakage or predation to which no answer is readily available. Brachials begin to become cuneate just distal to the cup and in most cases become biserial cuneate by about the 8th secundibrach; a few remain cuneate farther distally and none become rectilinear biserial.

Superfamily DIMEROCRINITOIDEA Zittel, 1879

Family DIMEROCRINITIDAE Zittel, 1879

This family is a regular component of crinoid faunas from Ordovician to Devonian and has been discussed by many authors (Ausich, 1986a; Brower, 1973; Breimer, 1962; Frest & Strimple, 1981; MacIntosh, 1981, 1987; Witzke & Strimple, 1981 among others). Since most that is known about this family comes from the Northern Hemisphere it is outside my aims to review its phylogeny. However, in adding the several Australian forms that follow I have had to make some inferences about Northern Hemisphere taxa. The simplest way to recognise members of the family until recently had been to identify that a crinoid was dicyclic and that its radials were all in contact except for interrupion by the primanal in the CD interray. Witzke & Strimple (1981) questioned the universality of this single feature and I agree with their discussion of evolution between the Rhodocrinitoidea and Dimerocrinitoidea. In assigning *Hollowaycrinus* to the Opsiocrinidae and suggesting that *Stelidiocrinus* may also belong to that family I follow their line of thought. I also follow Witzke & Strimple (1981) in the generic divisions of the family based on numbers of arms (Fig. 5) although there is good reason to believe that numbers of arms may have changed on several parallel lineages within the family.

Moving along Witzke & Stimple's (1981) ideas we now have available generic names for dimerocrinitoids with uniserial arms that divided once (*Duncanicrinus* gen. nov.), twice (*Nexocrinus* Eckert, 1984) or more than twice in each ray (*Ptychocrinus*) and for biserial representatives with 10 (*Dimerocrinites*), 20 (*Eucrinus*) or more than 20 arms (*Eudimerocrinites* (=*Ambicocrinus*), *Griphocrinus*). Whether latest Ordovician *Ptychocrinus fimbriatus*, Llandovery *P. longibrachialis* and Early Devonian *Duncanicrinus* constitute a lineage or not will only be answered by gaining further knowledge of Silurian taxa and thus detailed phylogenies but at present this is a reasonable hypothesis worth further testing (Fig. 5). These generic groupings accommodate Brower's (1973) idea that the 3 latest Ordovician species of *Ptychocrinus* represented 3 separate lineages and should be separated generically and Witzke & Strimple's (1981) ideas on the existence of 3 lineages in the Dimerocrinitidae based primarily on numbers of arms. There are no doubt numerous exceptions to these general groupings and the most obvious is the high probability that the transition from uniserial to biserial arms occurred more than once in each lineage. However, it is necessary to continue assimilating new data into an hypothesis

FIG. 4. *Hollowaycrinus calvus* gen. et sp. nov., all crowns with or without stem attached, from NMVPL229. A, NMVP107101, ×2.5. B, holotype, NMVP100158, ×4. C, NMVP100150, ×5. D, NMVP100153, ×4. E, NMVP107102, ×3.5. F, NMVP107104, ×3.5. G, NMVP107103, ×3. H, NMVP107099, ×5.

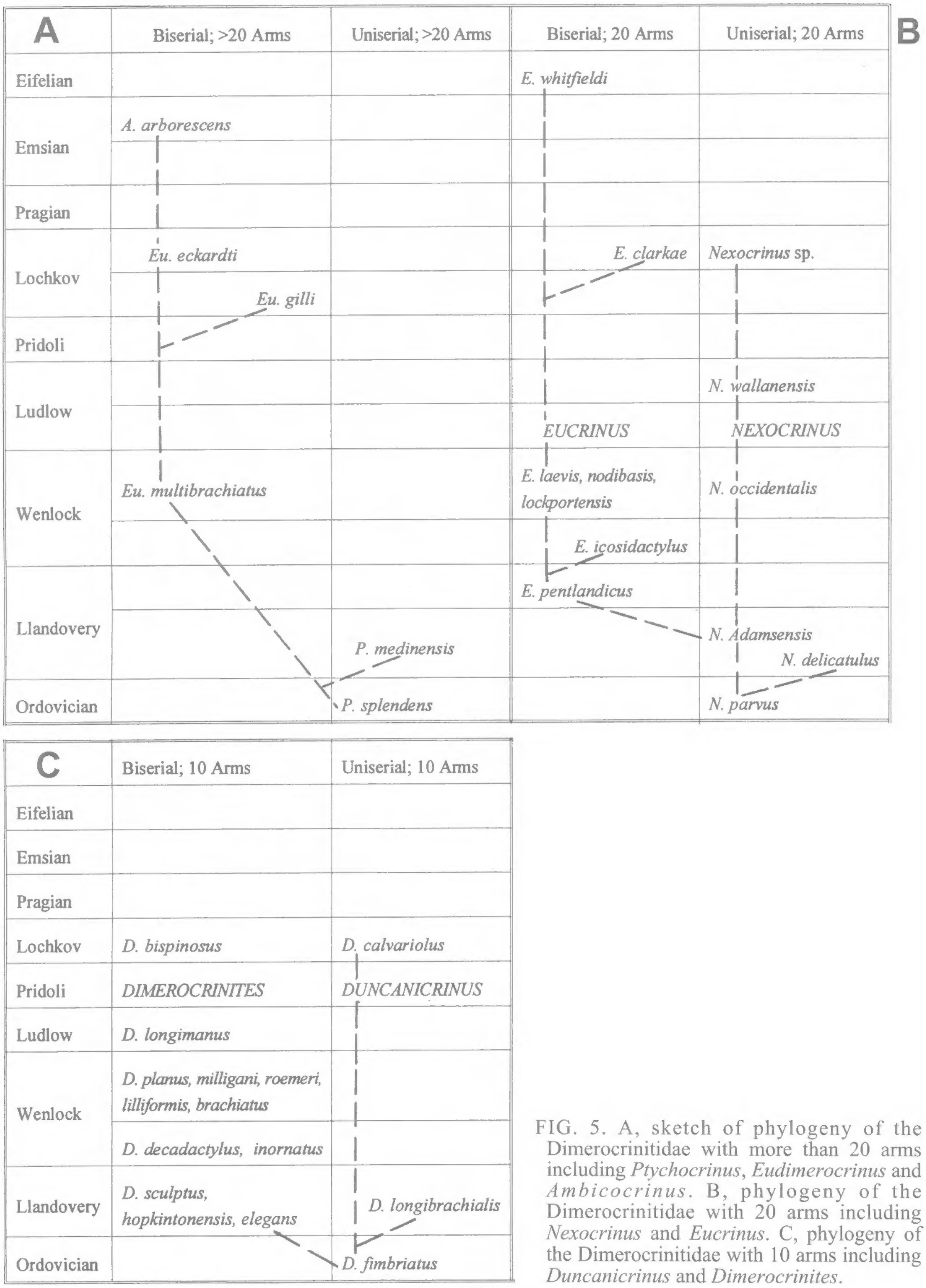



FIG. 5. A, sketch of phylogeny of the Dimerocrinitidae with more than 20 arms including *Ptychocrinus*, *Eudimerocrinus* and *Ambicocrinus*. B, phylogeny of the Dimerocrinitidae with 20 arms including *Nexocrinus* and *Eucrinus*. C, phylogeny of the Dimerocrinitidae with 10 arms including *Duncanicrinus* and *Dimerocrinites*.

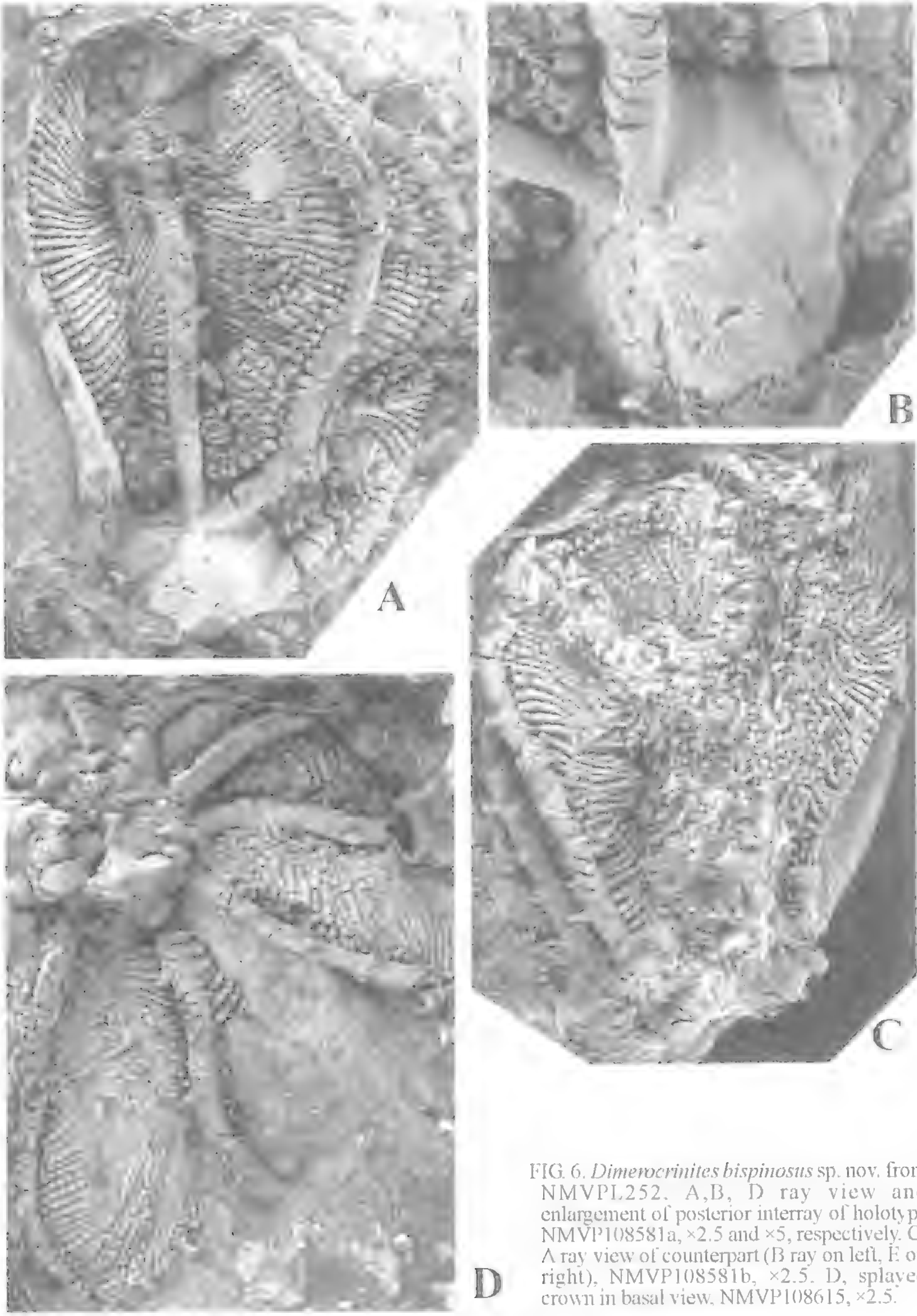


FIG. 6. *Dimerocrinites bispinosus* sp. nov. from NMVPL252. A,B, D ray view and enlargement of posterior interray of holotype NMVP108581a, ×2.5 and ×5, respectively. C, A ray view of counterpart (B ray on left, E on right), NMVP108581b, ×2.5. D, splayed crown in basal view, NMVP108615, ×2.5.

until all the details are worked out. To that end I offer a possible phylogeny (Fig. 5) for known species of Dimerocrinitidae for future testing and modification where necessary. Just how many lineages and which features remained constant to be able to recognise separate lineages remain largely unanswered for the dimerocrinitids today as when Witzke & Strimple (1981) raised many questions on the origins of their groupings.

**Dimerocrinites** Phillips in Murchison, 1839

TYPE SPECIES. *Dimerocrinites decadactylus* Phillips in Murchison, 1839 from the Wenlock of England; by subsequent designation of Roemer, 1855.

REMARKS. I apply the concept of Witzke & Strimple (1981) to *Dimerocrinites (Dimerocrinites)* which is to restrict the genus to those forms of the broader generic group with 10 arms.

**Dimerocrinites bispinosus** sp. nov.
(Fig. 6)

ETYMOLOGY. Latin *bi-*, two and *spinosus*, spine, for the pairs of spines on the outer sides of arms.

MATERIAL. HOLOTYPE: NMVP108581. PARATYPE: NMVP108615 from NMVPL252.

DIAGNOSIS. Ten arms, with prominent regularly spaced pairs of spines every fifth brachial on outer face, with hexagonal intersecundibrach, with low but distinct anitaxis of hexagonal plates.

DESCRIPTION. Crown subcylindrical, up to 45mm long, up to 4 times as long as wide. Cup subconical, about 1cm long, longer than wide, with convex tegmen; cup plates thin, smooth. Infrabasals concealed by stem. Basals pentagonal, except for hexagonal posterior one, with narrowest proximal margin forming part of circular rim to basal concavity, about as long as wide, with marked proximal medial projection (suggesting a pentagonal stem with the angles of the stem in the centres of basals beneath this projection), with Y-shaped median ray ridge dividing about midlength and extending onto adjacent radials. Radials heptagonal, much wider than long, with inverted Y-shaped ray ridge, with arms of this Y running onto adjacent basals. First 2 secundibrachs fixed in cup. Arms 10, of uniform cross section through available arm length; 1st primibrach hexagonal, not as wide as radial and little more than half as long; 2nd primibrach axillary, heptagonal; each arm uniserial with cuneate brachials as far as 6th or 8th secundibrach, biserial distally, with pair of strong solid spines on outer surface of rami placed about every 5 brachials; pinnules on each free brachial (i.e. distal to 2nd secundibrach) on each side of ramus, long, of 8-12 pinnulars. Interprimibrachs numerous, with heptagonal proximal one supporting 2 plates of about the same size, with size decreasing rapidly distally. First intersecundibrach hexagonal, subsequent plates not clear but presumably part of tegmen. Posterior interray with central anitaxis of hexagonal plates; hexagonal primanal supporting 3 anals in next row; anal plates numerous, decreasing distally, with average size smaller than that of interbrachials. Stem unknown.

REMARKS. With 10 biserial arms this species is placed in *Dimerocrinites* of Witzke & Strimple (1981) and is distinguished within that taxon by the spines on the outer arm faces, long hexagonal intersecundibrachs and the heptagonal axillary 2nd primibrach.

**Eucrinus** Angelin, 1878

TYPE SPECIES. *Eucrinus laevis* Angelin, 1878 from the Wenlock of Gotland; by subsequent designation of Wachsmuth & Springer, 1881.

REMARKS. This taxon is used in the sense of Witzke & Strimple (1981) to include species of *Dimerocrinites* with 20 arms; there seems little point in maintaining subgeneric distinction since we have no clear idea of phylogeny among these many species and when lineages are established it seems likely that both *Dimerocrinites* and *Eucrinus* will prove to be polyphyletic. The Victorian species is assigned on the basis that all rays countable have 4 arms except for one which has 5 and is considered aberrant; thus a total of 20 arms would be expected if branching is uniform.

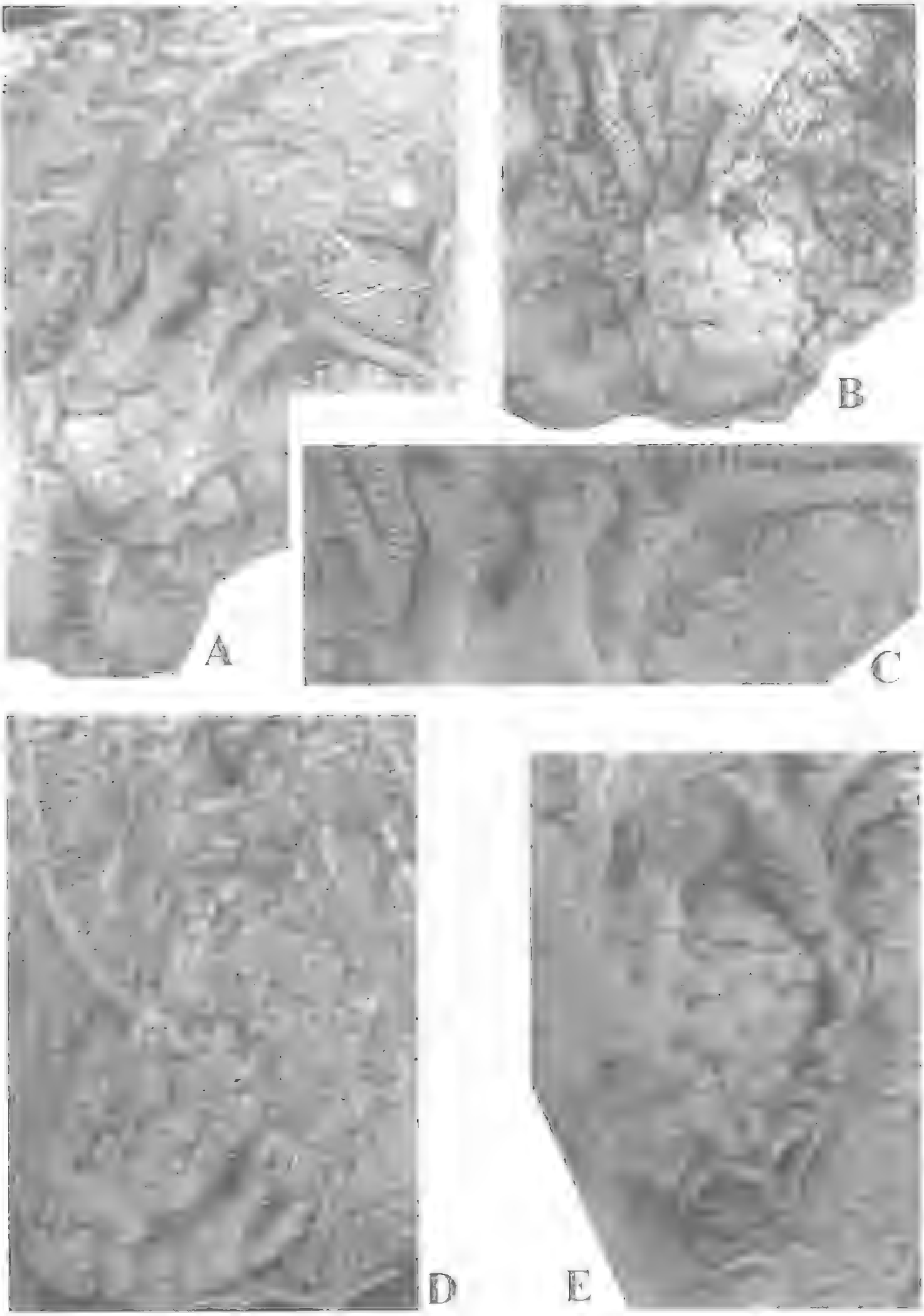
**Eucrinus clarkae** sp. nov.
(Fig. 7)

ETYMOLOGY. For Penny Clark who helped greatly with photography, curation and fieldwork.

MATERIAL. HOLOTYPE: NMVP108642. PARATYPES: NMVP108643, 108645 all from NMVPL252.

DIAGNOSIS. Basals, radials and radianal with distinctive coarse ornament of short fat radial

FIG. 7. *Eucrinus clarkae* sp. nov. all from NMVPL252. A,C, lateral view of crown with stem and enlargement of distal cup and proximal arms of NMVP108645a, ×2.5 and ×4, respectively. B, lateral view of NMVP108643, ×2. D, lateral view of NMVP108645b, ×2.5. E, CD interray view of holotype NMVP108642, ×4.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ridges normal to sutures and not joining centrally on plates. Crown with fine granulose ornament throughout. Intersecundibrachs few, in narrow vertical column, one in each row. Arms free distal to about 3rd tertibrach, uniserial proximally, secundibrachs becoming irregularly cuneate distally, tertibrachs becoming rectilinear biserial distal to about the 9th or 10th. Proximal brachials with distinctive fine ridge along proximal and distal margins. Stem round in section.

DESCRIPTION. Crown flaring gently distally, up to 60mm long. Cup high bowl-shaped, of large thin plates, up to 15mm long. Infrabasals concealed by stem (fragments evident in holotype between basals and stem but arrangement or number not available). Basals 5, with 4 of them pentagonal and posterior one larger and hexagonal, with proximal margin raised into prominent rim to basal cavity and stem, with conspicuous nodes representing ray ridges 2 per infrabasal directed towards middle of sutures with contiguous basals but 3 on posterior basal (central one vertical in middle of posterior interray). Radials 5, heptagonal except for hexagonal posterior one, largest plates in cup, with inverted Y-shaped ray ridges continuing from basals, with secondary radiating ridges horizontally onto adjacent radials. Primanal hexagonal, in radial circlet, supporting 3 anal plates distally, with prominent radial ridges near and normal to margins but not reaching centre of plate, lower central ridge from CD basal most prominent. Anal interray with large number of polygonal plates decreasing in size distally and only roughly in rows. First primibrach hexagonal, with broad low median ray ridge; 2nd primibrach axillary, heptagonal, with median ray ridge in Y-shape to enter 2 arms; 1st secundibrachs hexagonal, in sutural contact up middle of each ray, in contact with 1st intersecundibrach. Secundibrachs fixed in cup but protruding laterally, with 6th axillary, becoming cuneate distally. Arms free distal to about 3rd tertibrach, cuneate uniserial up to 6th tertibrach then biserial and pinnulate, tapering gently, longer than theca; pinnules long, slender, of at least 10 or more pinnulars, attached to each free brachial on both sides of each arm; interprimibrachs numerous, slightly depressed between fixed arms, with single large plate in contact with 2 radials and 1st primibrachs and supporting next row of 2 interbrachials, with more distal rows becoming much smaller and less regularly arranged; intersecundibrachs similar size to interprimibrachs at same height. Tegmen of many small polygonal plates (height of tegmen and anal opening not available). Stem circular, heteromorphic, with nodals higher and of greater diameter than internodals, noditaxis N1.

REMARKS. This species is distinguished within the genus by the distinctive ornament on the proximal theca, the large 1st secundibrach, the low ray ridges not occupying full width of fixed ray plates and the large flat hexagonal 1st interprimibrach. One half ray (Fig. 7A, C) has a normal branching on the 5th secundibrach then another branching on the 2nd tertibrach on the left division: this last branching is not seen anywhere else and is considered aberrant. The axillary tertibrach is cuneate with its long side in the Y of the previous division giving off the abnormal arm which then fills the Y of the previous division with 8-10 quite irregular, mostly cuneate brachials. The reason for this extra arm is not known.

### **Eudimerocrinus** Springer, 1926

TYPE SPECIES. *Eudimerocrinus multibrachiatus* Springer, 1926 from the Middle Silurian of Tennessee; by monotypy.

DIAGNOSIS. Cup subconical to deep bowl-shaped; basals with strong proximal projections. Arms 40, biserial in free section, with narrow ray ridges. Stem subpentagonal or at least not perfectly round in section.

REMARKS. In erecting this genus Springer (1926) identified the multiple arm branchings as the most significant feature. Ubaghs (1978b) maintained this feature and added a subpentagonal stem. In view of the new Australian species the projections of the basals may be another feature to add to the generic complex.

Witzke & Strimple (1981) placed *Eudimerocrinus* with *Ambicocrinus* Kirk, 1945 and *Griphocrinus* Kirk, 1945 in a group of dimerocrinitids with more than 20 biserial arms. The latter genus is generally distinguished by some if not all its radials being separated by

FIG. 8. *Eudimerocrinus eckardti* sp. nov. all from NMVPL229. A, incomplete specimen NMVP108951, ×1.5. B, partial cup and stem NMVP[illegible], ×2.5. C, D, part and counterpart of flattened crown NMVP[illegible] and [illegible], ×1.5. E, holotype crown NMVP109113, ×2. F, partial cup and inner side of arms from opposite side of cup NMVP109090, ×2.5. G, crown NMVP109168, ×2.5.

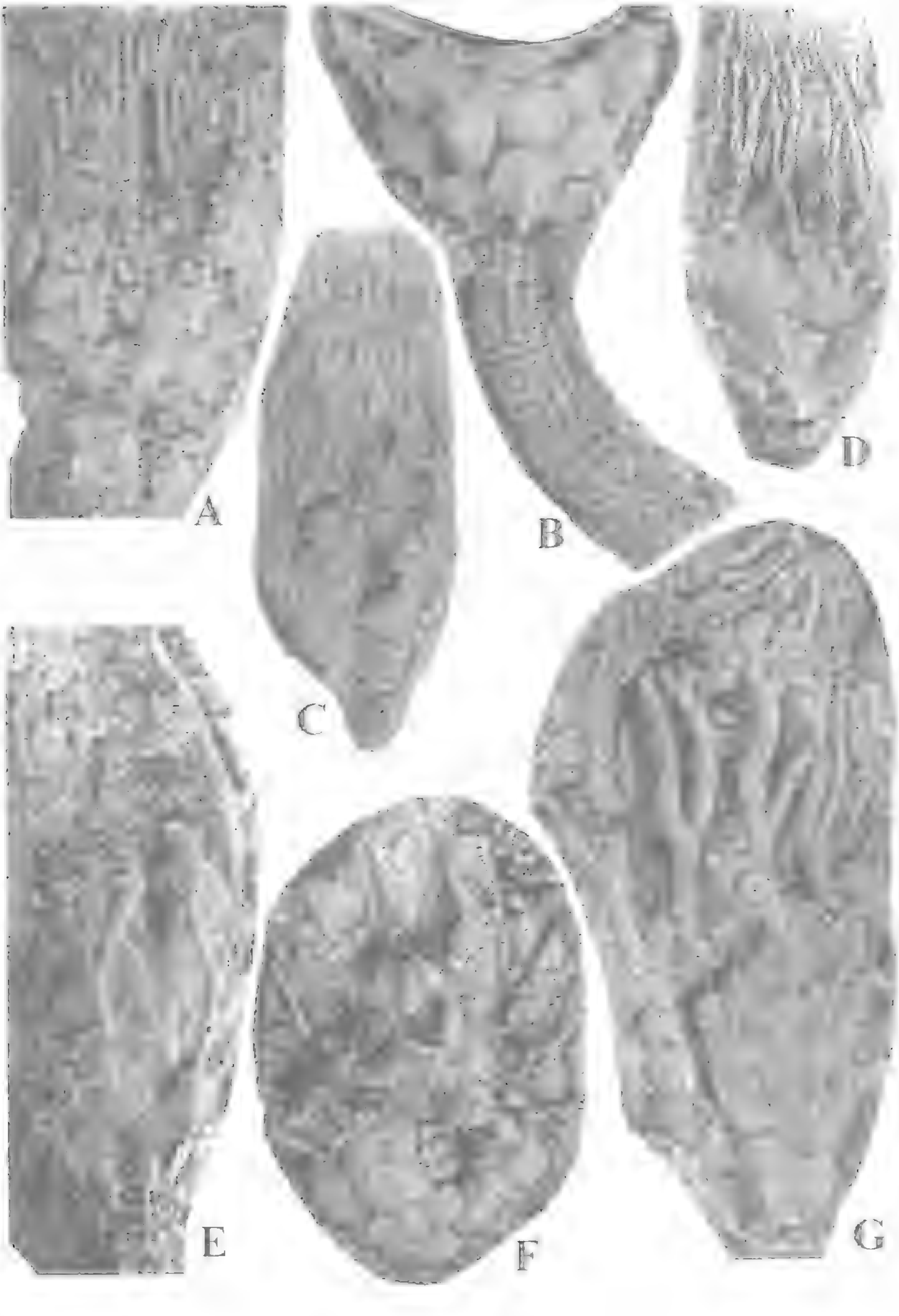
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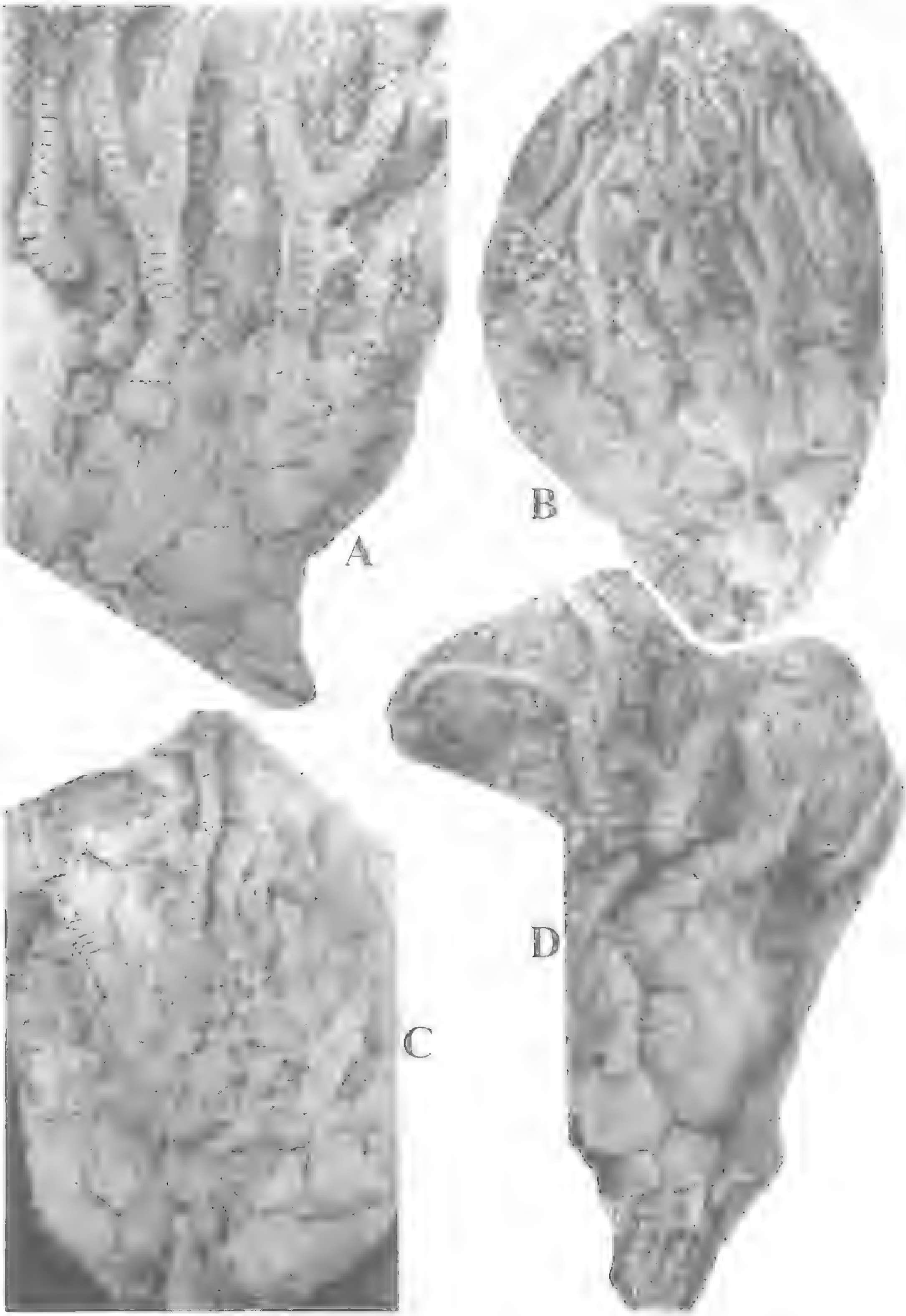
FIG. 9. *Eudimerocrinus eckardti* sp. nov. juveniles from NMVPL229. A, NMVP100492, ×4. B, NMVP110645, ×4.5. C, NMVP110647, ×2.5. D, NMVP149393, ×3.

interbrachials thus placing it intermediate between Rhodocrinitoidea and Dimerocrinitoidea and allowing separation from the other 2 genera; how a species of *Griphocrinus* with all its radials in contact could be distinguished from *Eudimerocrinus* is not clear. On the other hand distinction of *Ambicocrinus* is less certain; it has 40 biserial arms, subpentangular stem and identical cup plating arrangement. Goldring (1923:84) commented on the highly crushed preservation of and difficulty of illustrating the type, *A. arborescens* (Talbot,

FIG. 10. *Eudimerocrinus eckardti* sp. nov. A, partial cup and arms NMVP109767 from NMVPL252, ×2. B, partial cup and arms NMVP108689 from NMVPL229, ×2.5. C, partial cup and arms NMVP109768 from NMVPL252, ×2. D, distorted crown in posterior view NMVP108962 from NMVPL229, ×2.5.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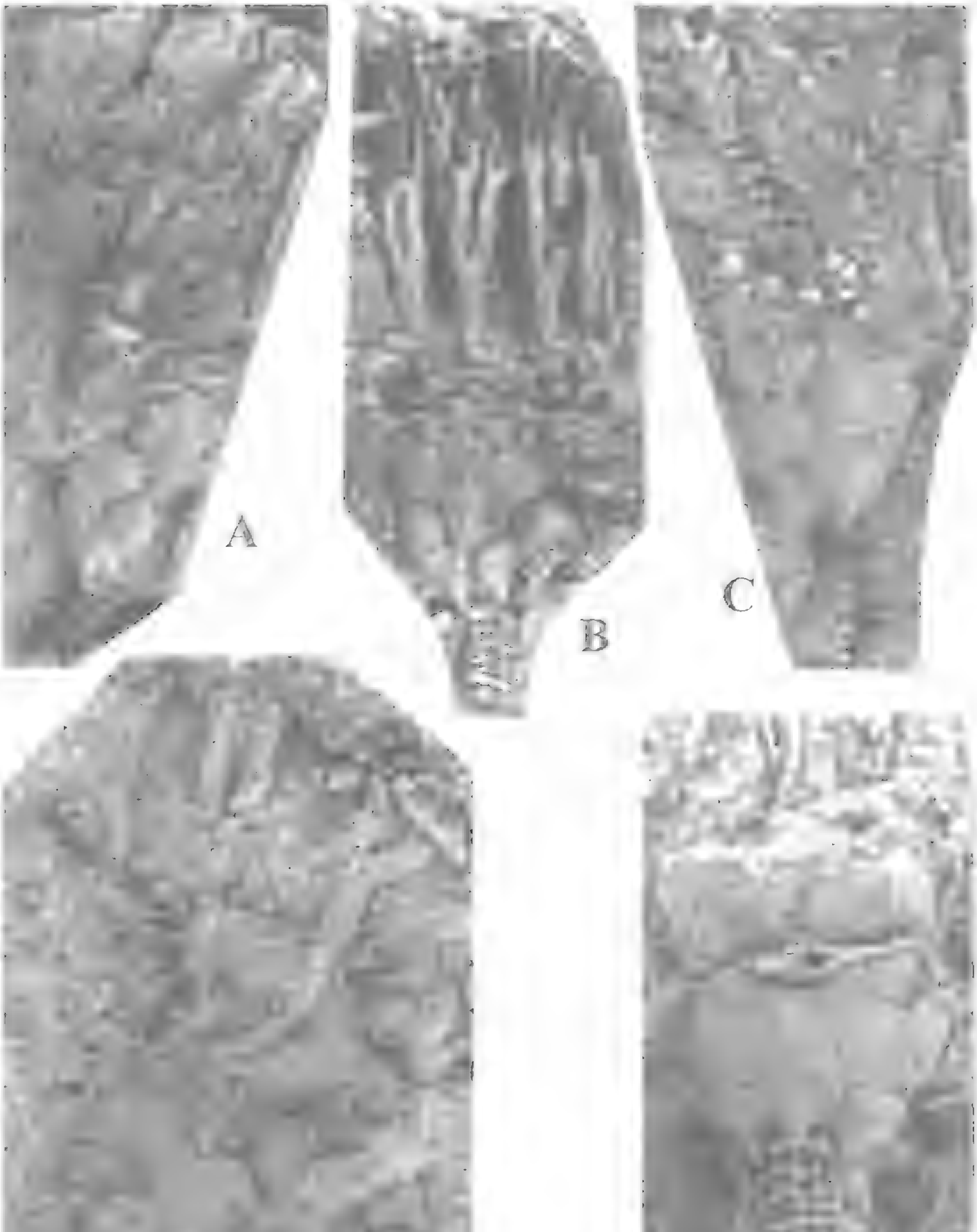
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1905), from the Lower Devonian (Lochkovian) of New York; she also noted its small size and indicated its depiction in her work was a reconstruction by the artist. Only the ray ridges and lack of projecting basals separate *A. arborescens* from *Eudimerocrinus* so given the circumstances noted by Goldring these could well be due to preservation or the artist's licence; I think it highly likely that *Ambicocrinus* is a junior synonym of *Eudimerocrinus* and that *Griphocrinus* may also prove to be synonymous when fully understood.

**Eudimerocrinus eckardti** sp. nov.
(Figs 8-11)

ETYMOLOGY. For Steve Eckardt who has rendered enormous field assistance and many specimens from his private collection.

MATERIAL. HOLOTYPE: NMVP109113. PARATYPES: NMVP100166, 100492, 108689, 108950, 108951, 108962, 108963, 109090, 109125, 109153, 109163, 109168, 109204, 110645, 110647, 149355, 149393 all from NMVPL229. Other specimens NMVP109221 and 109755 from NMVPL1924 and NMVP109767 and 109768 from NMVPL252.

DIAGNOSIS Basal plates with prominent proximally directed projections near lower margin; median ray ridges variably developed, often prominent; 1st primibrach hexagonal; 2nd primibrach axillary, heptagonal; arms 40, free distal to 4th-6th secundibrach; stem with distinctive decalobate cross section.

DESCRIPTION. Crown up to 55mm long, with cup and arms each about same length; cup up to 10mm long, high bowl-shaped, of large thin plates; infrabasals small, pentagonal, with conspicuous nodes on proximal margin (3 per infrabasal) in line with columns of lobes on stem. Basals 5, 4 hexagonal and CD basal heptagonal, largest plates in cup, with prominent proximally directed projections or spines medially near proximal margin, with spine extending beyond and concealing sutures between adjacent infrabasals, with faint median ray ridges in form of Y (Fig. 8E). Radials heptagonal, with inverted Y-shaped median ray ridge on most specimens, forming contiguous circlet around cup except in CD interray where hexagonal radianal intervenes in circlet; 1st primibrach hexagonal, with median ray ridge running in vertical line; 2nd primibrach axillary, heptagonal, with Y-shaped ray ridge into arms; 1st secundibrachs hexagonal, in sutural contact up middle of each ray, in contact with 1st intersecundibrach; first 6 secundibrachs fixed in cup; free arms biserial and pinnulate distal to 1st free secundibrach, branching approximately at secundibrach 10-11 and tertibrach 11-12, but branching often not at same level even in one ray, of relatively small diameter, tapering gently, approximately as long as theca; adoral groove wide and deep; pinnules long, slender, of at least 4-5 pinnulars, attached to each free brachial on both sides of each arm. Interprimibrachs numerous, not depressed between fixed arms, with single large plate resting on shoulders of 2 adjacent radials, with 2nd row of 2 plates, 3rd row of 3 plates level with top of primary axil, distally becoming much smaller and less regularly arranged with rows having 3-6 plates. Intersecundibrachs with 1st same size as interprimibrachs at same level. Anal interray wider than others, with primanal supporting 3 anals distally, subsequent anal plates without obvious order, decreasing in size to same extent as in interprimibrach series. Tegmen of many small vertically elongate plates, apparently quite long (almost as long as cup); anal opening not seen. Stem decagonal in section, heteromorphic, with noditaxis N3231323, with lobes aligned vertically in 10 columns to give stem appearance of fluted column with differential horizontal layering, no complete stem available.

MORPHOGENY. Small crowns (Fig. 11) have most of the cup occupied by the basals, radials, and first interbrachials, the diameter of the free arms compared to cup diameter is larger than the same ratio in large individuals and free arms are cuneate uniserial. These specimens are assigned to *A. eckardti* mainly because of the basal plate projections and similarity in every other feature available. These differences indicate that through growth the arms change from cuneate uniserial to cuneate biserial and then to rectilinear biserial; the arms do not increase in diameter at the same rate as the cup; and the cup increases in size in more distal parts with addition of interbrachial plates and greater growth there than in lower parts of the cup.

FIG. 11. *Eudimerocrinus eckardti* sp. nov. A, partial specimen with inner side of arms from opposite side of cup NMVP109221 from NMVPL1924, ×2.5. B, crown NMVP149355 from NMVPL229, ×2.5. C, cup and some arms NMVP109755 from NMVPL1924, ×3.5. D, cup and partial arms NMVP109204 from NMVPL229, ×2.5. E, cup and stem NMVP100166 from NMVPL229.

FIG. 12. *Eudimerocrinus gilli* sp. nov., holotype crown NMVP149345 from NMVPL1990, ×3.

REMARKS. This species is distinct within the genus in the detail of its stem, more subtle ray ridges and narrower arms relative to cup plates. It most closely resembles *A. arborescens* (type species of *Ambicocrinus* Kirk, 1945) from the Lower Devonian of New York which is distinguished by lacking the basal plate projections.

Two specimens from NMVPL252 (Fig. 10A, B) are assigned to this species but differ in having a subdued radial ornament on interprimibrachs, radials, primibrachs and secundibrachs and in having the second arm branching farther from the primaxil by about 4-6 brachials. They do have the projections on the basals and so are grouped with the material from NMVPL229 knowing that future material may show them to be part of a separate taxon.

**Eudimerocrinus gilli** sp. nov.
(Fig. 12)

ETYMOLOGY. For the late Edmund Gill for his geological work around Lilydale.

MATERIAL. HOLOTYPE: NMVP149345 from NMVPL1990.

DIAGNOSIS. Infrabasals barely evident in lateral view; basals with prominent rounded proximal projections; secundibrachs all fixed in cup; arms branching at least 3 times; stem subcircular to subpentagonal.

DESCRIPTION. Crown 32mm long, subcylindrical. Cup deep bowl-shaped, about 12mm long; cup plates thin, smooth except for prominent ray ridges. Infrabasals 5, mostly concealed by stem, upper tips just visible at top of stem between basals. Basals 5, hexagonal, except for pentagonal posterior one, with proximal margin forming part of circular rim to stem attachment, about as long as wide, with prominent well-rounded proximal projection, with median ray ridges emanating from the projections and running onto adjacent radials at right angles to interplate suture. Radials 5, heptagonal, wider than long, with inverted Y-shaped ray ridge. Arms apparently 40, with all primibrachs and secundibrachs fixed in cup, with free arms biserial, tapering distally; 1st primibrach hexagonal, not as wide or as long as radial, with median ray ridge across it; 2nd primibrach axillary, heptagonal, with Y-shaped ray ridge; secundibrachs 6, with median ray ridges, subquadrate or hexagonal; 6th axillary, with 2 round laterally (but not outwardly) declined facets; branching in free arms asymmetrical, with 6th tertibrach axillary in free arms of C and D rays immediately adjacent to CD interray but with next adjacent free arm in C ray having 12th tertibrach axillary and in D ray having 9th tertibrach axillary ( branching in A, B and E rays unknown). Interprimibrachs large, numerous, with proximal one supporting 2 plates of about the same size, with size decreasing rapidly distally; CD interray with 1st interprimibrach supporting 3 plates, wider than other interradial areas. First intersecundibrach hexagonal, supporting another 6-8 plates in 3 or 4 rows. Stem circular in section, noditaxis N212, with many low ossicles having wide epifacets (slightly wider in nodals than internodals).

REMARKS. Ubaghs (1978b) distinguished *Eudimerocrinus* from *Dimerocrinites* by its arms

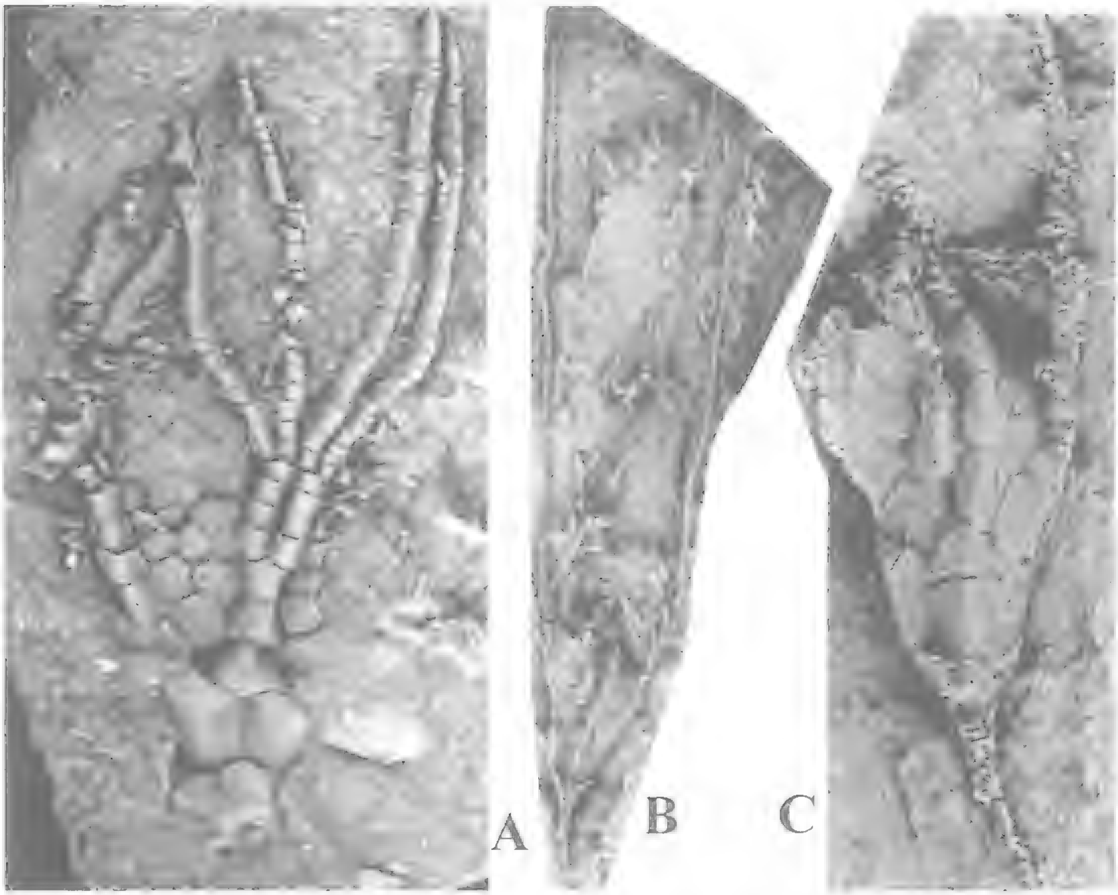



FIG. 13. *Nexocrinus wallanensis* sp. nov. from NMVPL1923. A, lateral view of holotype crown NMVP100116, ×3. B,C, posterior view of crushed crown (and enlargement of cup) NMVP107111, ×2 and ×5, repectively.

dividing several (presumably more than twice) times and its subpentagonal stem; *E. gilli* is thus assigned to *Eudimerocrinus*. It is distinguished from the genotype by the axillary secundibrachs being fixed in the cup, the cup being more bowl-shaped and the arms tapering more rapidly distally.

### **Nexocrinus** Eckert, 1984

TYPE SPECIES. *Nexocrinus delicatulus* Eckert, 1984 from the Llandovery of Ontario; by original designation.

OTHER SPECIES. *Ptychocrinus parvus* Hall, 1872 from the Upper Ordovician of North America; *Nexocrinus wallanensis* sp. nov. Ludlow of Victoria; *Dimerocrinites occidentalis* (Hall, 1863) from the Middle Silurian Waldron Shale of USA; *Nexocrinus* sp. Lochkovian of Victoria (herein); *Ptychocrinus adamensis* Ausich & Dravage, 1988 from the Llandovery of Ohio.

DIAGNOSIS. Cup conical; CD interray slightly wider than others; ray ridges prominent, may be subdued on proximal cup plates; infrabasals concealed by stem to long in lateral view. Posterior basal hexagonal, supporting primanal that separates C and D radials; arms 20, 4 per ray, uniserial, pinnulate, much longer than cup.

REMARKS. Brower (1973) dealt in detail with *Ptychocrinus* noting that the 3 Upper Ordovician species assigned are probably generically distinct. Eckert (1984) agreed that the genus was in need of revision and suggested that *P. parvus* should be removed because it had 20 arms unlike any other species included. He noted the similarity of his new genus to *P. parvus* but separated them on the number of fixed secundibrachs, width of the CD interray, distinctness of the anal ridge and plating of the posterior interray. Of these features the new Victorian species shares

with *N. delicatulus* the 4 fixed secundibrachs, the distinct anal ridge and the plating arrangement of the posterior interray. The only major distinction of the Victorian species is that its infrabasals are fully in view laterally and the ray ridges become less distinct proximally. I consider these to be interspecific differences and not of generic significance in the same way that the differences between *P. parvus* and *N. delicatulus* noted by Eckert (1984) distinguish those species within one genus. *Ptychocrinus adamsensis* Ausich & Dravage (1988) from the Llandovery of Ohio could be assigned to *Eucrinus* since it has 20 biserial (partially) arms. However, Ausich & Dravage (1988) made a good case for assigning it to the previously exclusively uniserial *Ptychocrinus*; they did not consider comparison with *Nexocrinus* which is a ptychocrinid genus with 20 uniserial arms distinguished by axillary 4th secundibrachs and some features of the posterior interradius. Since the posterior interradius of *adamsensis* is not available its features cannot be compared. However, the second division of the arms is at the 4th or 5th secundibrachs in *adamsensis* and I consider this species should be assigned to *Nexocrinus*. Ausich & Dravage (1988) argument that a species with uniserial proximal arms becoming biserial distally can belong to an essentially uniserial genus commands re-assessment of species with such arms. A single specimen from the Lower Devonian of Victoria with such arms, though they become biserial a little more proximally than in *adamsensis* and with 6th secundibrachs axillary, is assigned to this genus herein. That specimen is comparable to *Dimerocrinites occidentalis* (Hall, 1863) from the Silurian Waldron Shale of central USA on features of the cup but since arms are unknown for the latter species its assignment is equivocal.

**Nexocrinus wallanensis** sp.nov.
(Fig. 13)

ETYMOLOGY. From near the town of Wallen.

MATERIAL. HOLOTYPE: NMVP100116 and paratype NMVP107111 from NMVPL1923.

DIAGNOSIS Infrabasals long in lateral view; ray ridges prominent above the radials, becoming less distinct proximally. Primibrach 2 and secundibrach 4 axillary; arms fixed in cup up to about tertibrach 4 or 5. Arms 20, 4 per ray, uniserial, with primibrach 2 and secundibrach 4 axillary. Interrays with large number of polygonal plates (1 in first row followed distally by rows of 2, 3, 4 then irregular). Posterior interray with large basal longer than other basals; primanal directly distal, hexagonal, supporting 3 plates distally; prominent anal ridge medially on central column of vertically elongate hexagonal anal plates. Surface of plates smooth.

DESCRIPTION. Crown more than 60mm long, flaring distally. Cup high conical, with most of length in tegmen, with some tertibrachs fixed in cup. Infrabasals longer than radials, pentagonal, with highly obtuse angle distally. Basals hexagonal, large, largest plates in cup, with very faint broad ridges in X-shape crossing proximal and distal sides normal to margins. Radials heptagonal, in contact with adjacent radials except presumably in CD interray, with subtle ridges from basals continuing to meet medially near upper margin and continue as more prominent single ridge into brachials. First primibrach hexagonal, more convex in arm section distally; 2nd primibrach axillary, heptagonal, in contact with 2nd and 3rd rows of interbrachial plates; 4th secundibrach axillary; all secundibrachs and 2-3 tertibrachs fixed in cup. Free arms 4 per ray, with short fine pinnules, longer than cup, uniserial, with length of brachials decreasing gradually distally; pinnules one per brachial, alternating from side to side along arm. Interprimibrachs numerous, in regular rows of 1, 2, 3, 4, with 1st resting on shoulders of radials, with distally large number of irregular polygonal plates forming large but presumably not very competent tegmen; intersecundibrachs and intertertibrachs not clearly evident. Anal interray with basal longer than other basals, with distinct median ridge from infrabasal to tegmen; primanal and subsequent median plates long, hexagonal, with greatest width above midlength; other anal plates large, polygonal. Stem subcircular to subpentagonal in section, with pentagonal lumen.

REMARKS. This species is assigned to *Nexocrinus* on cup shape, ray ridges, shape of plates in the median anal column, 20 uniserial arms and depressed interprimibrachs. It is distinguished within the genus by the length of the infrabasals in lateral view. This species may ultimately prove to be generically distinct but in the present state of knowledge this is the most likely placement.

**Nexocrinus** sp.
(Fig. 14)

MATERIAL. NMVP149343 from NMVPL252.

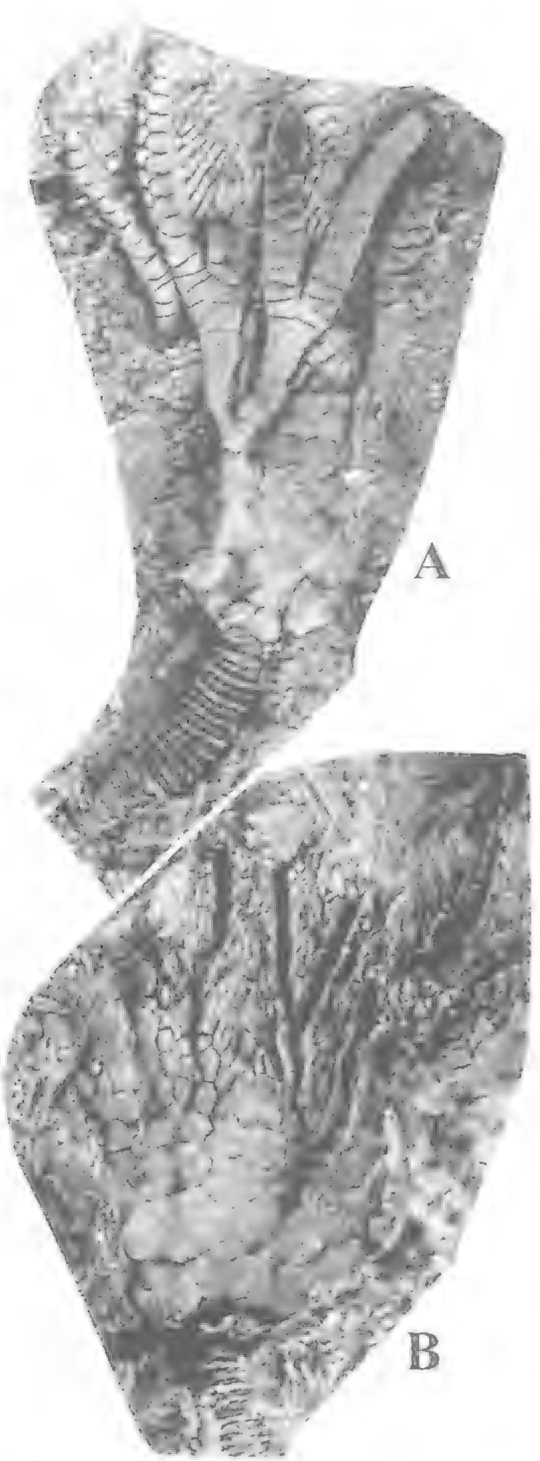



FIG. 14. *Nexocrinus* sp. incomplete crown in lateral view external (A) and internal (B) NMVP149343 from NMVPL252, ×4.

DESCRIPTION. Cup high conical, of thin plates, with median ray ridges well-developed, with radial ornament on interbrachial areas. Infrabasals 5, small, visible in lateral view, with ray ridges from adjacent basals meeting medially on the lower margin. Basals 5, hexagonal (posterior one presumably heptagonal and supporting 3 anal plates distally), smaller than radials, with cross of broad ray ridges from adjacent radials and infrabasals. Radials 5, heptagonal, much wider than long, with inverted Y-shaped ridges forking at midpoint of plate, with much thinner and lower ridges radiating from the midpoint to the middle of the other 4 sides. First primibrach hexagonal, wider than long, crossed vertically by prominent ray ridge, with faint lateral ridges from centre to sutures with interbrachials. Second primibrach pentagonal, axillary, with ray ridges occupying most of plate and dividing into both rami, with lateral marginal flange and upper tip depressed to interray areas. First secundibrachs and tertibrachs in contact laterally. Secundibrachs uniserial, cuneate, fixed, 6th axillary, with number of small long narrow intersecundibrachs up to level of 1st tertibrach. Tertibrachs cuneate for proximal 3 or 4 then biserial, with long pinnules on each brachial on each side of arm in biserial part (full length of arms not available).

Interprimibrachs numerous, 1 in first row more distal rows with 2, 3, 4, then becoming more elongate and less regular, with fine radial ornament. Anal interray unknown. Internal mould of cup with a groove in cup plates matching the position of the ray ridges, beginning on the radials, becoming deeper and narrower upwards onto the arms, suggesting that similar though shallower and less distinct grooves branched from the 3rd secundibrach out and up across lateral interprimibrachs. Stem circular in section, noditaxis N1, of very low ossicles of uniform length but with epifacet of nodals of greater diameter than that of internodals.

REMARKS. This specimen resembles *Dimerocrinites occidentalis* (Hall, 1863) from the Silurian Waldron Shale of Indiana with which it shares the infrabasals well exposed in lateral view, narrow ray ridges, fine radial ornament on interbrachials and fine longitudinal ornament on the ray ridges. However, it may be distinguished by its larger diameter stem (relative to thecal diameter), the ray ridges on basals in an X rather than a Y as in *occidentalis* and its 20 arms as opposed to the 10 surmised in *occidentalis*. No illustrated specimen of *D. occidentalis* is complete in the arms distal to about the 2nd

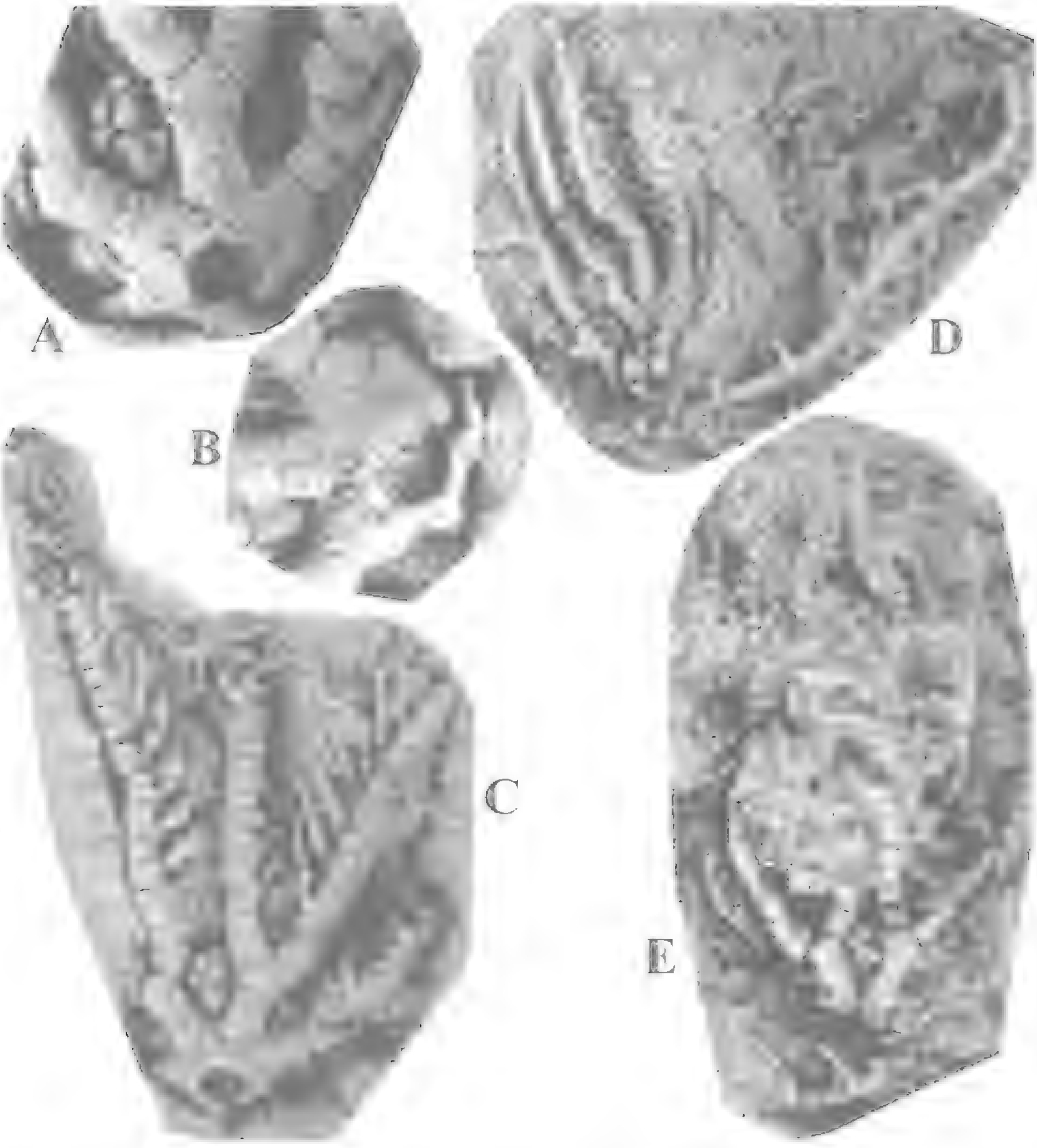


FIG. 15. *Duncanicrinus calvariolus* gen. et sp. nov. A-C, NMVP110649 from the rubbish tip on Watson's Road, Pheasant Creek, Kinglake. A, E ray enlarged view of cup, ×10. B, enlarged basal view of cup with posterior basal at 12 o'clock, ×10. C, crown in E ray view with distal arms incomplete, ×5. D,E, part and counterpart of slightly disarticulated NMVP108647 from NMVPL252, ×4.

secundibrach. This Australian specimen illustrates that the second division of the arms is on the 5th or 6th secundibrach so it is quite possible that the arms of *D. occidentalis* may have divided a second time to produce 20 arms. Until the arms of this North American species are known the comparison must remain incomplete but I suggest it is more likely that *occidentalis* belongs to *Nexocrinus* than to *Dimerocrinites* or *Eucrinus*.

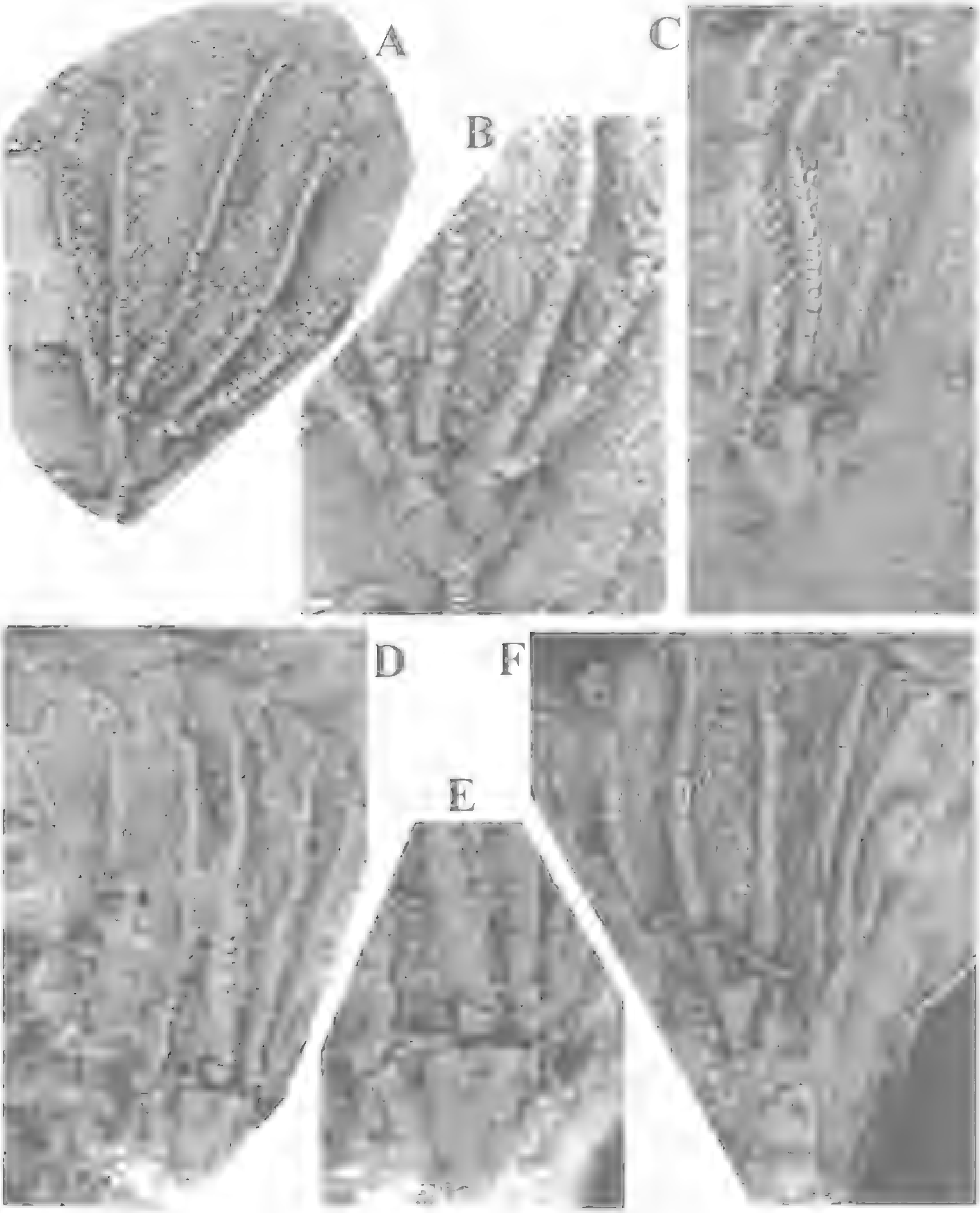



FIG. 16. *Duncanicrinus calvariolus* gen. et sp. nov., all crowns from NMVPL252. A,B, NMVP108640, ×4 and ×6, respectively. C, NMVP108634, ×5. D,E, NMVP108617, ×6. F, NMVP108633, ×2.5.

**Duncanicrinus** gen. nov.

TYPE SPECIES. *Duncanicrinus calvariolus* sp. nov.

ETYMOLOGY. For Peter Duncan of the Whittlesea district, a benefactor of Victorian palaeontology.

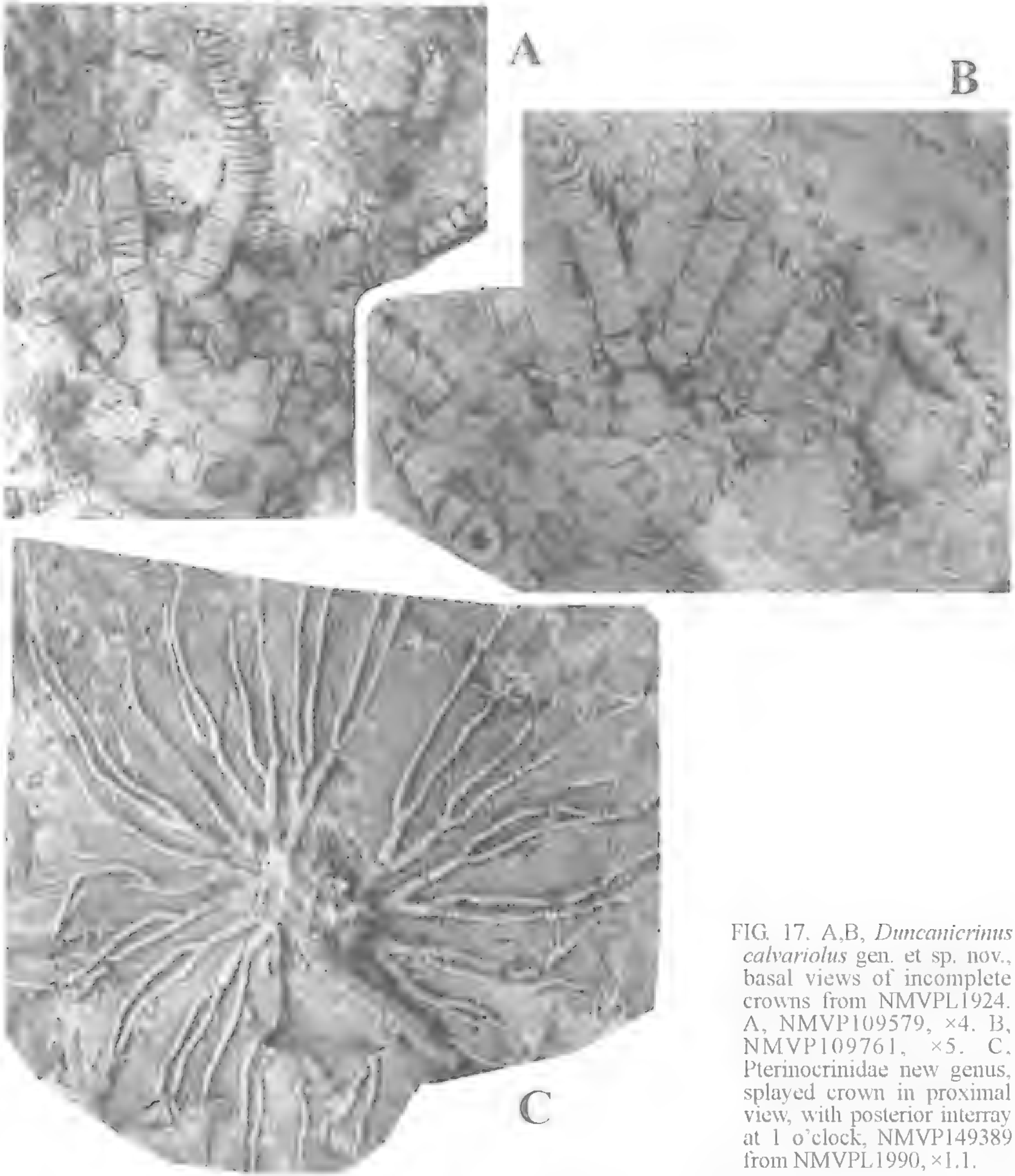



FIG. 17. A,B, *Duncanicrinus calvariolus* gen. et sp. nov., basal views of incomplete crowns from NMVPL1924. A, NMVP109579, ×4. B, NMVP109761, ×5. C, Pterinocrinidae new genus, splayed crown in proximal view, with posterior interray at 1 o'clock, NMVP149389 from NMVPL1990, ×1.1.

OTHER SPECIES. *Ptychocrinus fimbriatus* (Shumard, 1855) from the Ordovician of USA; *Ptychocrinus longibrachialis* Brower, 1975 from the Silurian of Scotland.

DIAGNOSIS. Cup conical, of smooth or tuberculate plates, with or without ray ridges. Infrabasals 5, pentagonal, concealed by stem attachment or partially visible in lateral view. Basals 5, hexagonal; posterior basal longer than others, reaching more than halfway up radials. Radials in lateral contact except in posterior interray. Interprimibrachs few, beginning with one resting on radials. Tegmen of small polygonal plates. Arms 10, uniserial, of cuneate brachials, with long pinnules on prominent facets

alternating along arm. Stem circular, noditaxis N3231323, some with cirral spines at noditaxis base.

REMARKS. Brower (1973) noted that within the Dimerocrinitidae the 3 Ordovician species of *Ptychocrinus* could be regarded as belonging to separate genera. In discussing phylogeny he suggested that the forms with 10 arms may belong to one lineage and could have given rise to the 10 armed *Dimerocrinites*. Accepting Brower's (1973) phylogeny the Victorian species is placed with *Ptychocrinus fimbriatus* in a genus characterised by 10 uniserial arms that was foreshadowed by Jell (in Jell & Holloway, 1983) in discussion of the holotype, then the only known specimen. *Macarocrinus* Jaekel, 1895 is a related genus but its type, *M. springeri* Jaekel, 1895 has 15 arms and is considered generically separate. Species of *Macarocrinus* with 10 arms should probably be transferred to *Duncanicrinus* but detailed study of those species is outside the scope of this paper.

**Duncanicrinus calvariolus** sp. nov.
(Figs 15-17)

Dimerocrinitidae gen. et sp. nov. Jell in Jell & Holloway, 1983:12, figs 7C-E, 8

ETYMOLOGY. Latin *calvariola*, small cup.

MATERIAL. HOLOTYPE: NMVP74246 from the floor of Winneke Reservoir, Christmas Hills, E of Melbourne described and figured by Jell (in Jell & Holloway, 1983:12, figs 7C-E, 8) as Dimerocrinitidae gen. et sp. nov. PARATYPES: NMVP110649 from the rubbish tip on Watson's Road, Pheasant Creek, Kinglake and NMVP108617, 108633, 108634, 108640, 108647 all from NMVPL252. Other material NMVP109579, 109761 and 109763 from NMVPL1924.

DIAGNOSIS. Cup very small, of smooth plates, without ray ridges. Infrabasals may or may not be visible in lateral view. Interprimibrachs few, maximum of 6-8 per interray. Arms free distal to primaxil. Stem cirriferous.

DESCRIPTION. Crown up to 30mm long, strongly flared in proximal part then subcylindrical, with arms more than 5 times as long as cup. Cup very small (about 2mm across and 1.5mm long), conical, of smooth thin plates, with shallow sharply rimmed stem facet. Infrabasals 5, completely concealed by stem (Fig. 15B), just visible laterally as wide low triangle (Jell & Holloway, 1983, fig. 7C) or fully visible and pentagonal (Fig. 15D). Basals 5, usually hexagonal, maybe pentagonal with proximal margin slightly curved and forming sharp margin to basal concavity, occupying up to 60% of cup length, with acute distal tip at point where radials begin to descend into interradial depressions; posterior basal heptagonal, supporting primanal above horizontal suture, remainder of anal sac uncertain but apparently with median anitaxis of hexagonal plates. Radials 5, heptagonal, contacting each other laterally through lateral flanges in interradial depressions; radial facet peneplenary (c.0.8 of radial width), horizontal, subcircular in section. Each primibrach with lateral flanges in interradial depression in line with those on radials. Arms 10, with axillary 2nd primibrach, free distal to primaxil, of cuneate secundibrachs, with long pinnules alternating side to side along each arm; each pinnule of 8 pinnulars. Interprimibrachs convex, in regular rows 1, 2, 3 distally. Stem circular in section, noditaxis N3231323, with nodals each bearing stout cirri.

REMARKS. The specimen from Winneke Reservoir is now fully interpretable with discovery of the several specimens from different localities all just to the NE of Melbourne. This species is distinguished from *D. fimbriatus* by its smaller cup, fewer smaller interprimibrachs and cirriferous stem. There is some variation within the species in the amount of the infrabasals visible laterally, in the interbrachials and in the shape of the brachials but none of this variation can be considered interspecific. The discussion of the holotype provided by Jell (in Jell & Holloway, 1983) indicated close relationship to *Ptychocrinus* and this is confirmed here with closest relationship to *Ptychocrinus fimbriatus* now assigned to *Duncanicrinus*.

Family PTERINOCRINIDAE McIntosh, 1987

**Pterinocrinid** gen. nov.
(Fig. 17C)

MATERIAL. NMVP149389 from NMVPL1990.

DESCRIPTION. Crown splayed on bedding plane, approximately 50mm in diameter. Cup low bowl-shaped (probably more conical originally and now shortened by compaction), with plate margins not discernible; ornament of prominent ray ridges. Infrabasals not discernible. Basals presumably 5, not discernible except posterior one intervening between C and D radials; posterior basal 5-sided, with strong central boss and 5 radiating ridges to centre of each side. Radials 5, 5-sided, with 2 ray ridges from centre

of 2 proximal sides meeting at centre of plate then running to centre of distal side; C and D radials with extra ridges to anal X. Posterior interray wider than others; anal X large, resting on basal, separating C and D radials, supporting 3 anal plates, with ray ridges running vertically and 2 running diagonally from adjacent radials; distal anal plates not clearly defined but with strong tubercles or short spines. Arms 40 (if branching is regular; E ray appears to have one branch missing the 3rd division and another with a 4th division - maintaining the 8 branches for the ray but irregularly; C and D rays branching regularly); primibrachs 2, with 1st hexagonal, with 2nd pentagonal and axillary; secundibrachs not readily countable due to preservation but approximately 5 or 6, 3 or 4 fixed in cup; free brachials with raised proximal and distal marginal rims leaving a distinct groove at midlength, each with 2 long slender pinnules, one on each side of arm; pinnules with more than 6 pinnulars each. Stem pentagonal in section, with angles of stem aligned with ray ridges bisecting proximal margin of each basal, heteromorphic, with lateral extremities of each columnal at 5 stem angles appearing to be curved distally (possibly due to preservation).

REMARKS. Although infrabasals are not clear there are many dimerocrinitoids in which they are concealed by the stem and the plate arrangement is not characteristic of monocyclic camerates. I therefore, infer concealed infrabasals. The compound biserial brachials assign the taxon to the Pterinocrinidae within this superfamily and the prominent ray ridges separate it from all other members of the family except *Apurocrinus* McIntosh (1981) from which it is distinguished by its different branching pattern. McIntosh (1987) described cornice-shaped rims along distal lips of free brachials in the other South American Devonian pterinocrinid *Bogotacrinus scheibei*; its brachials are thus very similar to those of the Victorian taxon where a similar rim also occurs on the proximal lip. *Bogotacrinus* is also comparable in having a pentagonal stem in the same relationship to the basal circlet. However, *Bogotacrinus* lacks strong ray ridges and has a different arm branching pattern. Relatively poor preservation of the single specimen available precludes application of a formal name so I retain the new taxon in open nomenclature. Although McIntosh (1979) described the columnal in the stem facet as round, his figure (McIntosh, 1979, fig. 5.1) clearly shows it to be subpentagonal with each angle at the centre of the proximal edge of a basal.

Order MONOBATHRIDA
Moore & Laudon, 1943
Suborder COMPSOCRININA Ubaghs, 1978
Superfamily HEXACRINITOIDEA
Wachsmuth & Springer, 1885
Family HEXACRINITIDAE
Wachsmuth & Springer, 1885

**Hexacrinites** Austin & Austin, 1843

TYPE SPECIES. *Platycrinites interscapularis* Phillips, 1841 from the Middle Devonian of England; by monotypy.

REMARKS. This genus is widespread throughout the Devonian of Australia (Philip, 1961 - L. Dev.; Jell et al., 1988 - M. Dev.) This is the first species with upper arms preserved and with unweathered plate surfaces.

**Hexacrinites chirnsidensis** sp. nov.
(Fig. 18)

ETYMOLOGY. From Chirnside Park, an outer suburb of Melbourne, near Lilydale.

MATERIAL. HOLOTYPE: NMVP107097. PARATYPES: NMVP107095, 107096, 107098, 107100, 110644 all from NMVPL1922.

DIAGNOSIS. Low but distinct median ray ridges on all cup plates except primanal; 1st primibrach and 4th secundibrach axillary; 4 arms per ray. Stem circular; columnals almost as high as diameter, with protruding flange near midlength.

DESCRIPTION. Crown up to 25mm long, conical proximally, less flared distally. Cup high conical, of unornamented plates except for ray ridges. Basals 3, equal, symmetrically beneath A, C and D radials, with a median ray ridge centrally on A basal leading onto A radial, with 2 other ray ridges from A basal continuing onto B and E radials, with 2 median ray ridges on each of other 2 basals continuing onto B, C and D, E radials, respectively (Fig. 18A), with distinct rim around stem attachment giving rise to ray ridges. Radials 5, up to twice as long as wide, each with distally decreasing median ray ridge; radial facet about 1/2 radial width, declivate, semicircular to horseshoe-shaped on outer but only weakly convex on interior. Primanal same size as radials, smooth, without ray ridge or facet. Arms 20, 4 per ray, uniserial, with deep groove on inner side of each. First primibrach axillary, pentagonal; secundibrachs 4 per arm, 4th axillary, subquadrate in lateral view, almost circular in section except for

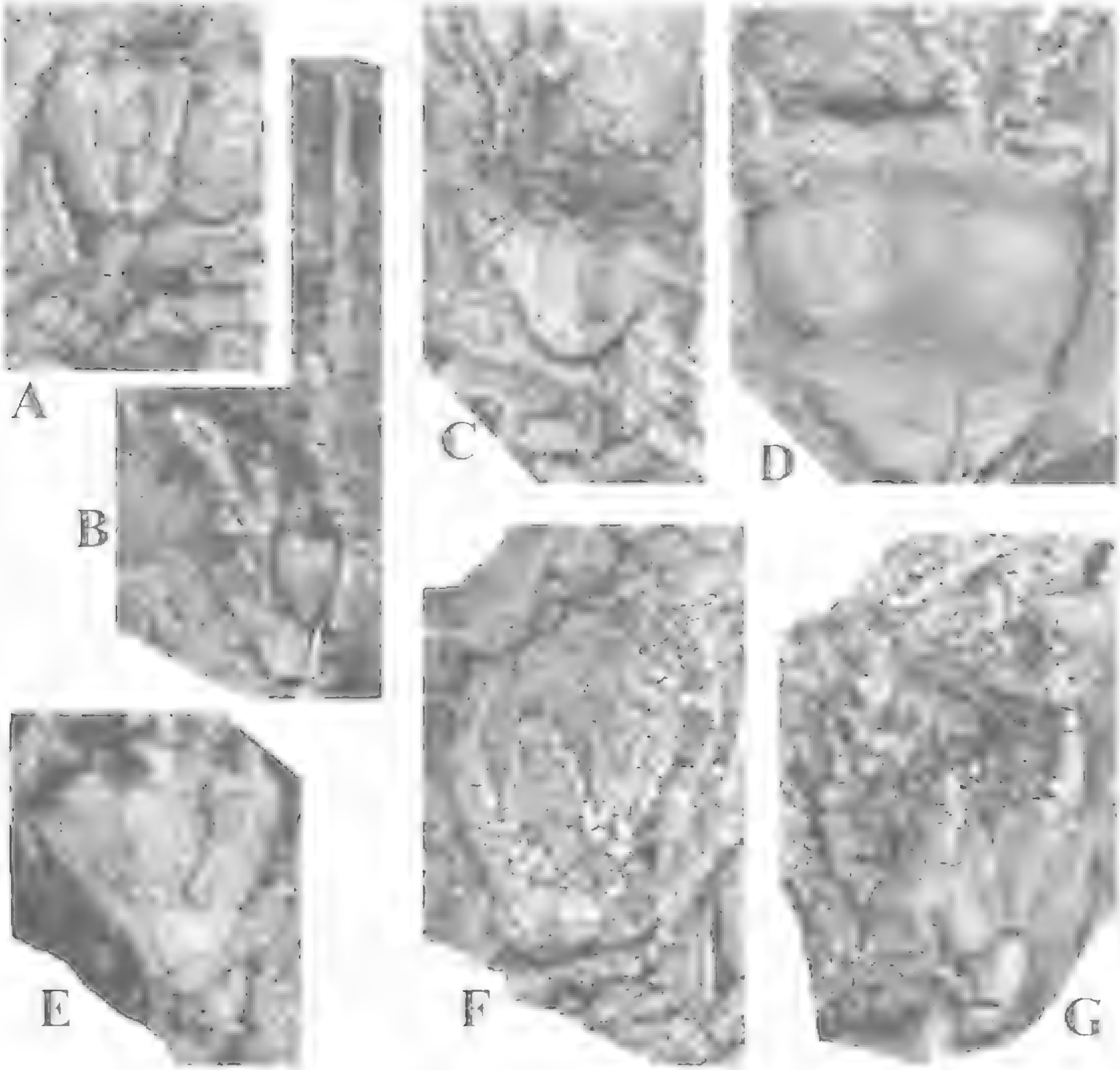


FIG. 18. *Hexacrinites chirnsidensis* sp. nov., all incomplete crowns from NMVPL1922. A,C, part and counterpart of holotype NMVP107097, ×3.5 and ×4, respectively. B,G, part and counterpart of NMVP107098, ×4. D, internal mould (not a latex cast) of NMVP107095, ×5. E, NMVP107100, ×6. F, NMVP107096, ×2.5.

groove on inner side, apparently not pinnulate; tertibrachs becoming cuneate distally, with large well-developed facet for attachment of pinnules; pinnules one per brachial, alternating from side to side up each arm (distal extent of arms not available). Single large plate of tegmen adjoining radials between radial facets. Stem circular in section, with strongly crenulate sutures between columnals throughout, heteromorphic proximally; proximal section of short columnals with lateral flange at midlength, with flange slightly wider on nodals; distal section of uniform columnals, long (as long as 4 proximal columnals), with lateral midlength flange occupying only small part of length of columnal.

REMARKS. Most species of *Hexacrinites* have some obvious and distinctive ornament on the basal and radial plates; a few are smooth (some illustrated specimens may be smooth through postmortem weathering) but none of the smooth species have the subtle ray ridges of *H. chirnsidensis*. A similar species is *Arthroacantha vega* Prokop, 1982 which shares the very long basals,

subtle median ridge ('considerably convex, especially in their middle parts' Prokop, 1982) on radials but not on radianal and horizontal depression of radial plates just proximal to distal margin. It is distinguished by the tuberculate ornament which is the only feature that could be used to assign the Czech species to *Arthroacantha*. However, numerous species of *Hexacrinites* have tuberculate ornament and I suggest that *A. vega* probably belongs to *Hexacrinites* closely allied to *H. chirnsidensis*. Similar also is the specimen of *Hexacrinites* described by Philip (1961) which is available as an interior mould having a distinct median convexity, a horizontal groove just proximal to the distal margin and long conical shape all the same as in *H. chirnsidensis*; it is quite possible that Philip's specimen and the Chirnside Park material are conspecific.

**Oehlerticrinus** LeMenn, 1975

TYPE SPECIES. *Oehlerticrinus sellloucnsis* LeMenn, 1975 from the Lower Devonian of France; by original designation.

REMARKS. LeMenn (1975) erected this genus for 5 species for hexacrinitids with strongly and distinctively ornamented cup plates, with 2 primibrachs, with organised interbrachial plating, with compound brachials and with a cirriferous stem. The last 2 features are evident in only one species each and their occurrence in the other species are inferred. Although the 2 species added herein have uniserial arms and non-cirriferous stems they are assigned to this genus because 1) basic cup plate ornament is evident though less striking; 2) there are 2 primibrachs; 3) the primanal supports 3 plates; and 4) a single large interbrachial rests on adjacent radials and is surrounded distally by small polygonal plates. Of other hexacrinitids with 2 primibrachs *Arthroacantha* Williams, 1883 from the Devonian of Europe and North America has spines articulated on tubercles on the cup and biserial arms that branch 3 times and lacks a linear cup plate ornament. *Platyhexacrinus* Schmidt, 1913 from the Devonian of Europe and Siberia is similarly distinguished except that it lacks the cup spines and has a very inflated tegmen, while *Prohexacrinus* Yakovlev, 1946 from the Silurian of the Urals also has a subglobose cup and almost equidimensional radials. When the stem and arms are known for all species the variation here inferred may suggest further subdivision but at present assignment to *Oehlerticrinus* is considered most likely.

**Oehlerticrinus lemenni** sp. nov.
(Figs 19, 20)

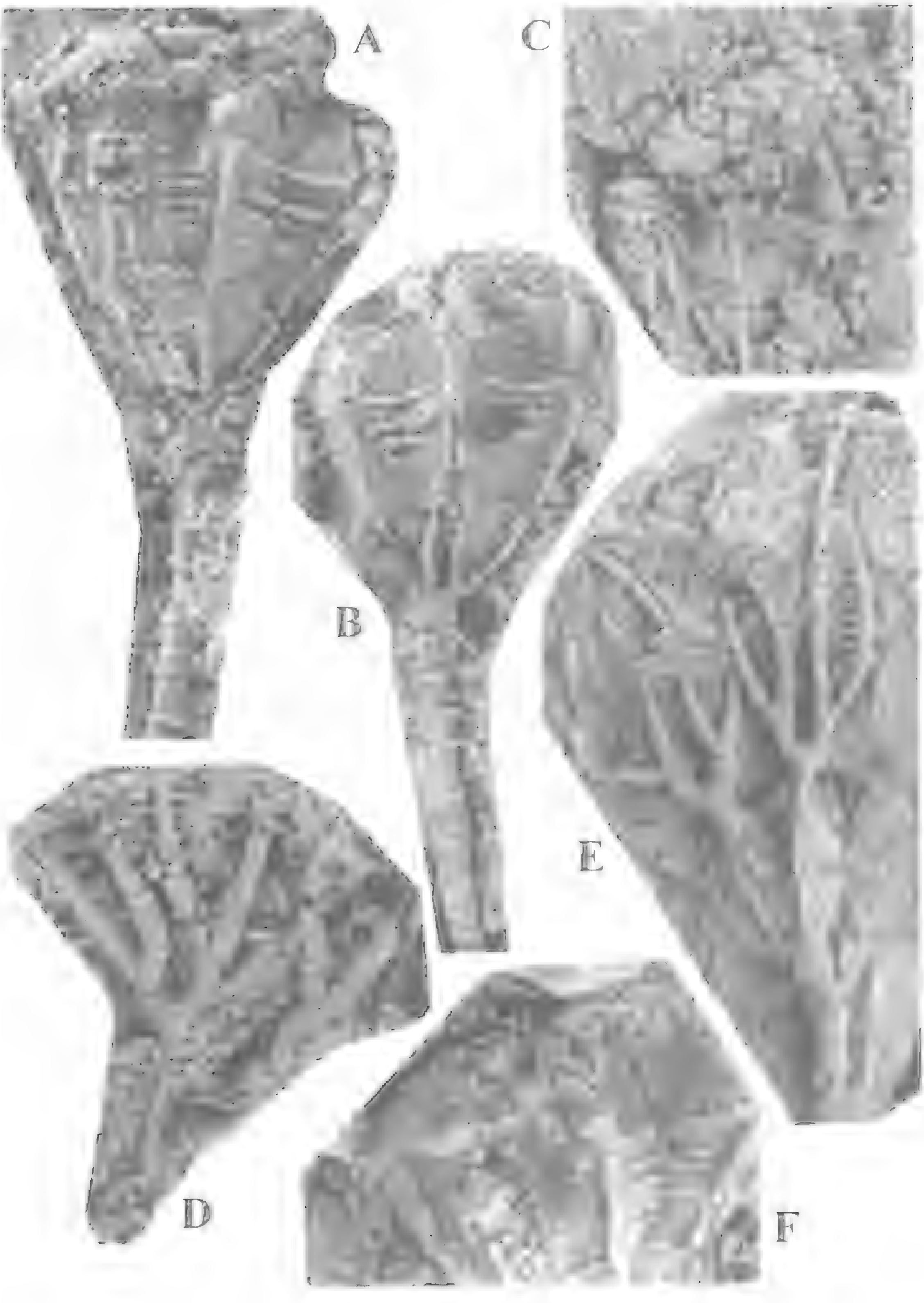
ETYMOLOGY. For Jean Le Menn, the author of the genus.

MATERIAL. HOLOTYPE: NMVP109213. PARATYPES: NMVP109098, 109116, 109164, 109166, all from NMVPL229. NMVP108672, 108679 and 108682 from NMVPL252.

DIAGNOSIS. Cup high conical. Ornament of strong narrow ray ridges single on A, C, and D radials, double on B and E radials and primanal, with slightly less prominent sharp horizontal ridges around the cup at height of radial facet and just proximal to it, with background ornament of fine tubercles over entire cup. Tegmen with 5 large subtriangular interambulacrals surrounded orally by small irregular ambulacrals. Arms 20, rectilinear uniserial. Stem circular in section, heteromorphic with strongly crenulate intercolumnal suture, with columnals becoming longer distally.

DESCRIPTION. Crown up to 48mm long, with arms flaring distally and more than twice as long as cup. Cup high conical, consisting of basals, radials and primanal. Basals 3, equal, forming hexagonal circlet, symmetrically beneath A, C and D radials, occupying about 30% of cup length, each with 3 ridges radiating from distinct rim around stem attachment and crossing each of 3 distal edges. Radials 5, up to twice as long as wide, about 70% of cup length, with narrow sharp ridges continuing from basals, with similarly narrow and sharp horizontal ridges running around the cup at height of facet and just proximal to it, horizontal ridges fading out on approach to vertical ridges, with background of fine tubercles over entire cup; A, C and D radials with single median vertical ridge; B and E radials and primanal each with 2 ridges quite close together and converging on base of radial facet; radial facet about 1/4 radial width, declivate, semicircular to horseshoe-shaped. Primanal same size as radials, smooth, without facet but with strong tubercle at point where 2 vertical ridges meet, with single ridge continuing from this tubercle to distal margin, with distal margin

FIG. 19. *Oehlerticrinus lemenni* sp. nov. all from NMVPL229. A,B,F, holotype cup and stem NMVP109213. A, lateral C ray view, ×4. B, lateral A ray view, ×4. F, oblique posterior tegminal view, ×7. C, lateral C ray view NMVP109098, ×3. D, partial crown NMVP109164, ×4. E, crown NMVP109116, ×2.5.


A
B
C
D
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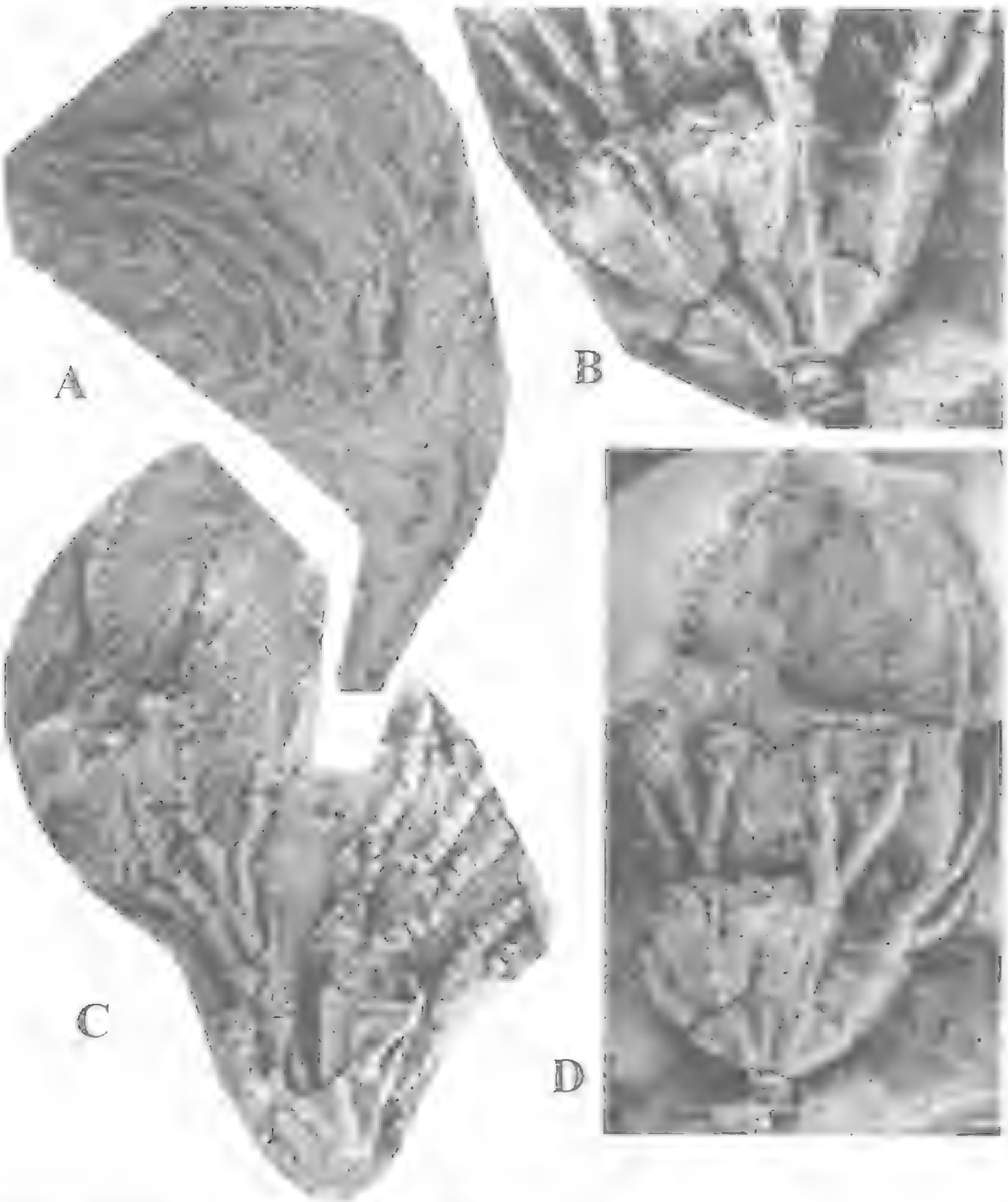
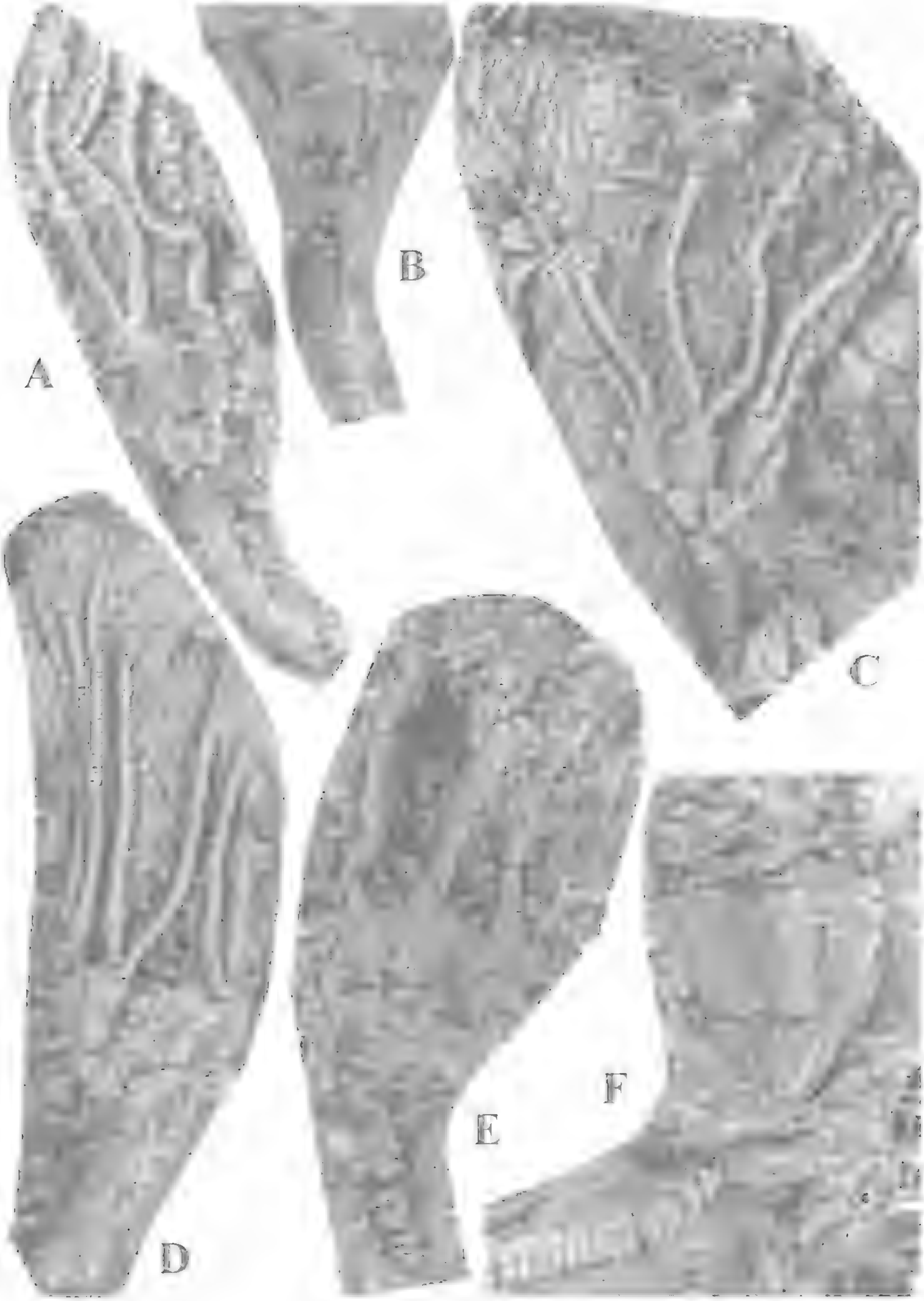



FIG. 20. *Oehlerticrinus lemenni* sp. nov. all from NMVPL252. A, crown with indistinct preservation of cup plates NMVP108682a, ×2.5. B,D, enlargement of cup and crown NMVP108679, ×6 and ×4, respectively. C, crown NMVP108672, ×5.

FIG. 21. *Oehlerticrinus jeani* sp. nov., all crowns (B and F with arms missing) from NMVPL252. A, NMVP108613, ×2.5. B, NMVP108664, ×3.5. C, holotype NMVP108626a, ×2.5. D, NMVP108614, ×2.5. E, NMVP108666, ×4. F, NMVP108618, ×6.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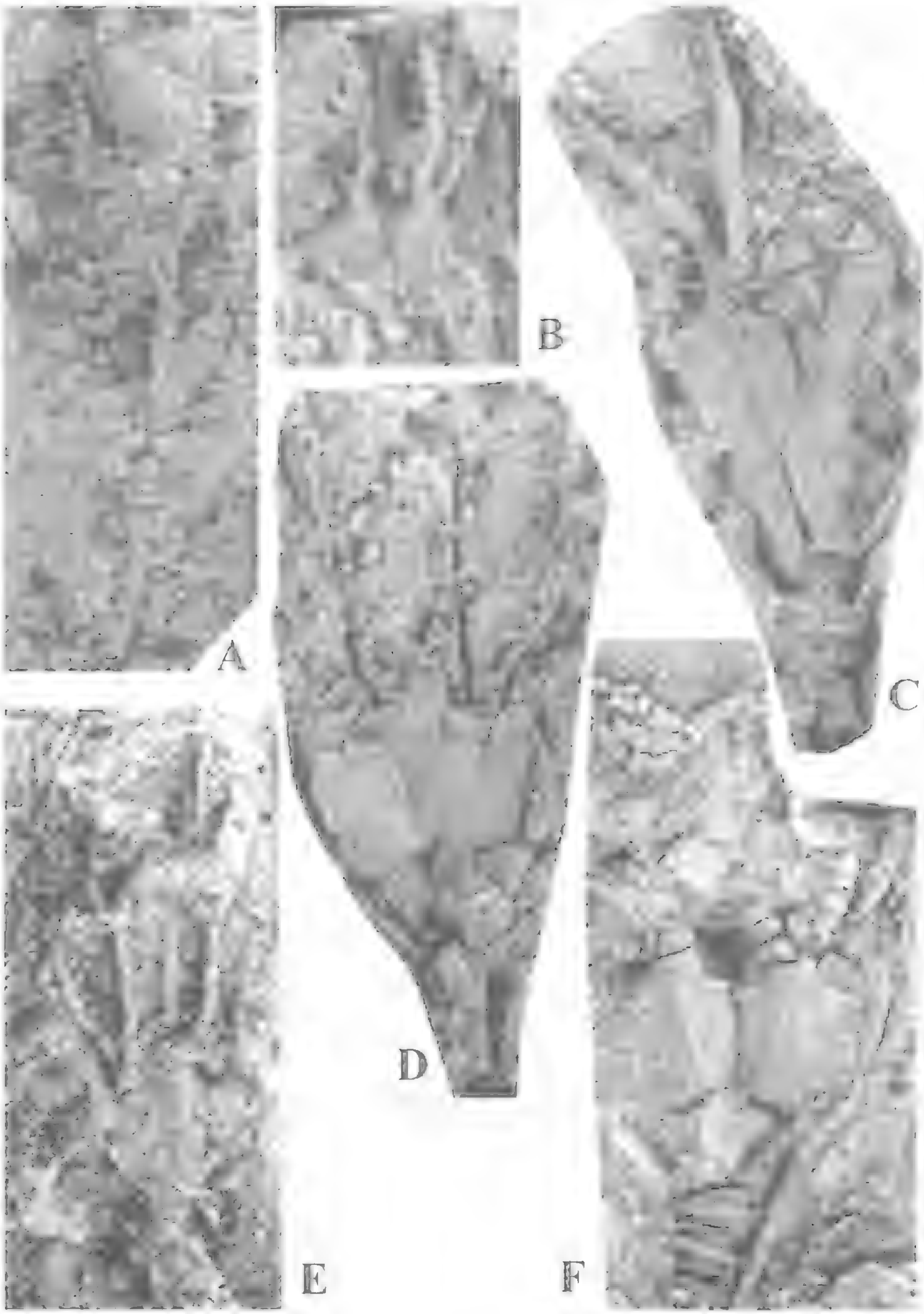
A
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of 2 straight sections, supporting 2 large anal plates. Arms 20, 4 per ray, rectilinear uniserial, usually with fine close-spaced longitudinal ridges, more than twice as long as cup. Second primibrach axillary, pentagonal; secundibrachs 4 per arm, 4th axillary, subquadrate in lateral view, almost circular, apparently not pinnulate; tertibrachs becoming cuneate distally, with large well-developed facet for attachment of pinnules; pinnules one per brachial, alternating from side to side along each arm. Tegmen with 5 large subtriangular interambulacral plates each resting symmetrically on 2 radials, with small irregular ambulacrals. Stem circular in section, with strongly crenulate sutures between columnals throughout; proximal section of low columnals with lateral flange at midlength, with flange slightly wider on nodals, noditaxis N212; distal section with longer (as long as 2 proximal columnals) columnals, with lateral midlength flange occupying only small part of length of nodals; internodals without lateral flange; noditaxis N1.

REMARKS. This species is distinguished from European members of the genus by its ornament, uniserial arms and noncirriferous stem. It is separated from *O. jeani* sp. nov. by its ornament and by its 20 rather than 10 arms.

**Oehlerticrinus jeani** sp. nov.
(Figs 21, 22)

ETYMOLOGY. For Jean Le Menn, the author of the genus.

MATERIAL. HOLOTYPE: NMVP108626. PARATYPES: NMVP 108613, 108614, 108618, 108664, 108666. 108667, 110641, 149375, 149376 all from NMVPL252; NMVP109150 from NMVPL229.

DIAGNOSIS. Cup ornament of low narrow ray ridges single on A, C, and D radials, double on B and E radials and radianal, with slightly more prominent horizontal ridge around the cup just proximal to radial facet and incomplete at each facet, with secondary ornament of fine broken wavy linear ridges parallel to the main ridges. Primanal supporting 3 anal plates. Arms 10, uniserial, of cuneate brachials. Stem circular in section, heteromorphic with strongly crenulate intercolumnal suture, with columnals becoming longer distally.

DESCRIPTION. Crown up to 35mm long, subcylindrical, arms at least 3 times as long as cup. Cup high conical, consisting of basals, radials and primanal; cup plates with ornament of fine, often wavy ridges, occasionally anastomosing, sometimes incomplete and then almost tubercular, subparallel to main ray ridges and thus forming more or less triangular patterns between midlines of adjacent radials and line joining adjacent radial facets. Basals 3, equal, forming hexagonal circlet, symmetrically proximal to A, C and D radials, occupying about 1/3 of cup length, each with 3 ridges radiating from distinct rim around stem attachment. Radials 5, up to twice as long as wide, occupying about 2/3 of cup length, with narrow ray ridges continuing up from basals, with narrow horizontal ridge running around the cup just proximal to facet but usually incomplete at the midline of radials; A, C and D radials with single central ridge; B and E radials and primanal each with 2 ridges converging on base of radial facet; radial facet about 1/3 radial width, declivate, semicircular to horseshoe-shaped. Primanal same size as radials, without facet, with single vertical ridge continuing distal to level of radial facets to distal margin medially, supporting 3 anal plates distally. Arms 10, 2 per ray, uniserial; 2nd primibrach axillary, pentagonal; secundibrachs becoming cuneate, with large well-developed facet for attachment of pinnules; pinnules 1 per brachial, alternating from side to side along each arm, of 6-10 pinnulars. Tegmen with 5 large subtriangular interambulacrals each resting symmetrically on 2 radials, with small polygonal ambulacrals. Stem circular in section, with strongly crenulate sutures between columnals; proximally low columnals with lateral flange at midlength, with flange slightly wider on nodals, noditaxis N212; distal section of uniform columnals, longer (as long as 2 proximal columnals), with lateral midlength flange occupying only small part of length.

REMARKS. *Oehlerticrinus jeani* is distinguished from European species by its ornament, its 10 uniserial arms and its noncirriferous stem. It is distinguished from the closely related and co-occurring *O. lemenni* under that species above.

Available specimens have been crushed so that many plates have disslocated at sutures while

FIG. 22. *Oehlerticrinus jeani* sp. nov. A, crown NMVP108667 from NMVPL252, ×3. B, juvenile crown NMVP149375, from NMVPL252, ×4. C,D, external and internal of NMVP149376, ×3. E, crown NMVP109150 from NMVPL229, ×4. F, cup with some arm fragments (counterpart of Fig. 21C), holotype NMVP108626 from NMVPL252, ×4.

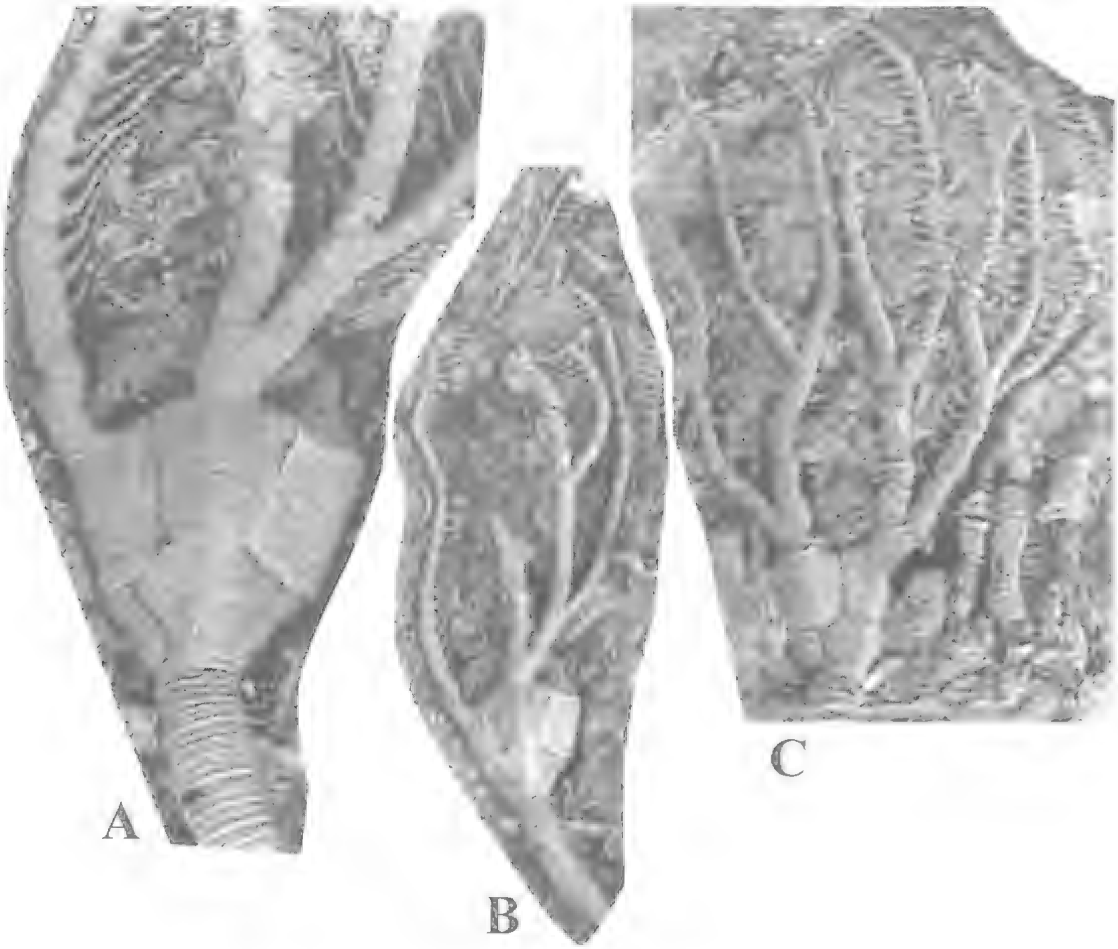



FIG. 23. *Frankocrinus holmesi* gen. et sp. nov. crowns from NMVPL229. A,B, holotype in D ray view NMVP109099, ×4 and ×1.4. C, NMVP109109, ×3.

others have fractured across the plate itself; this is particularly so near the upper margins of radial plates suggesting numerous reentrants into the radials. However, I have been unable to discern any clear pattern and maintain that the upper margins of the radials formed a smooth circle above which the tegmen was sutured.

## **Frankocrinus** gen. nov.

TYPE SPECIES. *Frankocrinus holmesi* sp. nov.

ETYMOLOGY. For Frank Holmes of Melbourne.

DIAGNOSIS. Cup high conical, of smooth or finely ornamented plates. Radials with broad low ray ridges and horizontal flexure at level of radial facets, distal to which radials depressed between arms. Second primibrach axillary. Arms fixed in cup up to about 2nd or 3rd secundibrach. Single large interprimibrach extending proximally to level of radial facet in large excavation of distal corners of adjacent radials. Arms 20, uniserial, pinnulate. Stem circular in section, with crenulate intercolumnal sutures.

REMARKS. This genus is assigned to the Hexacrinitidae on the basic cup pattern of plates proximal to the radial facets. However, distal to the radial facets the arms are fixed in the cup which extends distally >1/2 length of the radials even though depressed between the arms. I suggest that this genus represents a further development from *Oehlerticrinus* in which the radials extend distal to the radial facets and there is a large interprimibrach resting on the straight upper margin of the radials; extension of the

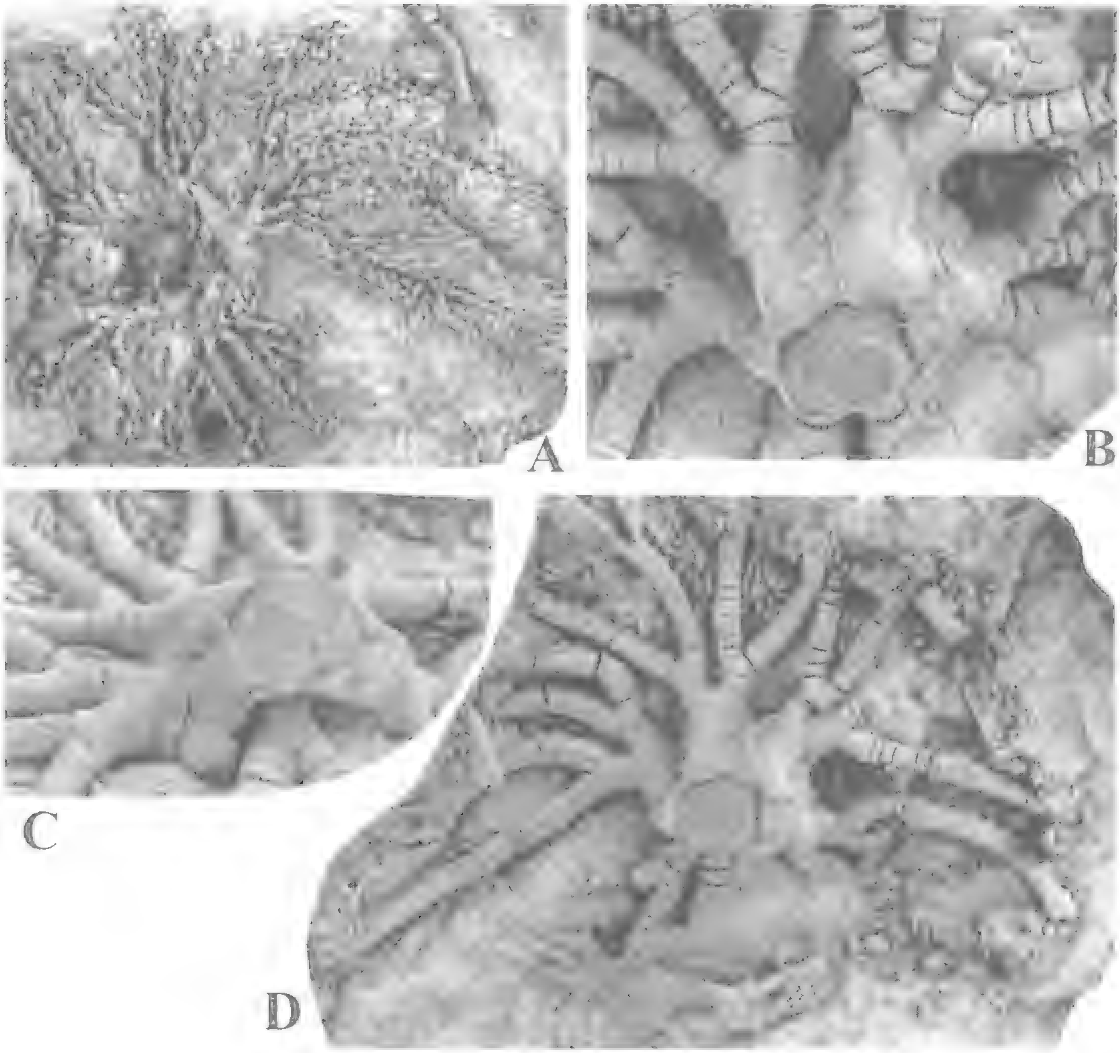



FIG. 24. *Frankocrinus enidae* gen. et sp. nov. splayed holotype crown NMVP108571 from NMVPL252. A, distal view of crown showing inner sides of arms, ×2. B, basal view with A ray at 11 o'clock, ×4. C, lateral view with cup inverted; D ray crushed under cup in forground, ×4. D, basal view with A ray at 12 o'clock, ×2.

interprimibrach proximally between the upper corners of the radials, radials smaller relative to size of cup than in other hexacrinitids and arms fixed in cup at least to the 2nd secundibrach are distinctive features of this genus. A comparable genus is *Cerasmocrinus* Strimple & Levorsen, 1973 from the Upper Devonian of Iowa in which the cup is typically hexacrinitid up to the radial facets and the arms are fixed in the cup and separated by a few large interprimibrachs up to at least the 1st secundibrach; that genus is separated from *Frankocrinus* by its flat wide primibrachs and 3 or more plates rather than one separating the fixed arms.

**Frankocrinus holmesi** sp. nov.
(Fig. 23)

MATERIAL. HOLOTYPE: NMVP109099. PARATYPE: NMVP109109 from NMVPL229.

DIAGNOSIS. Cup of smooth plates, with broad low angulation of the cup in position of ray ridges, with marked flexure around the cup at level of radial facet. Arms 20, fixed in cup up to 2nd secundibrach, uniserial, pinnulate, of

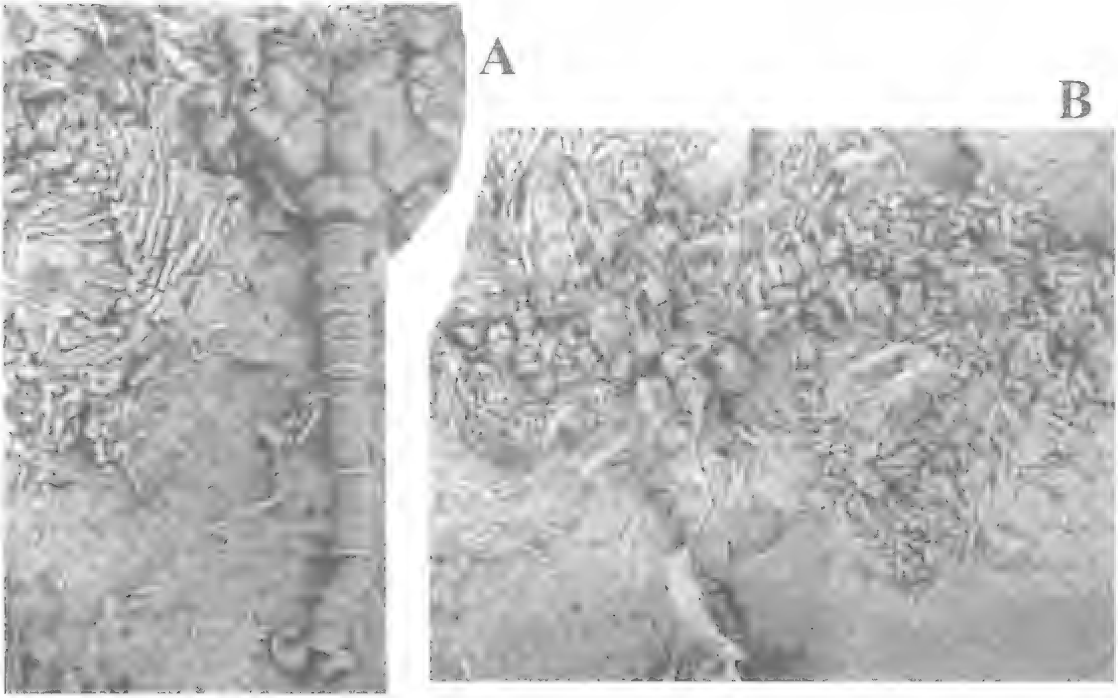



FIG. 25. *Frankocrinus enidae* gen. et sp. nov. part and counterpart of paratype cup and stem in posterior view, with disarticulated arms above the cup NMVP108622 from NMVPL252, ×3.5.

cuneate brachials. Fixed arms separated by depressed areas each occupied by a single large interprimibrach, with a number of smaller tegmenal plates above that. Stem circular in section, heteromorphic, with crenulate intercolumnal sutures.

DESCRIPTION. Crown up to 45mm long, conical to subcylindrical. Cup high conical, consisting of basals, radials and primanal; ray ridges low, broad, indistinct. Basals 3, equal, forming hexagonal circlet, symmetrically beneath A, C and D radials, occupying about 1/3 of cup height, each with vertical median ridge. Radials 5, only slightly longer than wide, occupying about 2/3 of cup length, with broad low ridges continuing from basals; A, C and D radials with single central ridge; B and E radials and primanal each with 2 ridges converging on base of radial facet; radial facet a little more than 1/3 radial width, almost horizontal, subsemicircular, proximal to the distal margin of radial. Primanal same size as radials, smooth, supporting 3 large plates. Arms 20 or more, uniserial, more than 4 times as long as cup. Second primibrach axillary, pentagonal; secundibrachs 6-10 per arm, cuneate, almost circular in section, pinnulate; tertibrachs cuneate, pinnulate, with large well-developed facet for attachment of pinnule on longer side; pinnules one per brachial, alternating from side to side along each arm, long, well spaced. Tegmen of small polygonal plates. Stem circular in section, with strongly crenulate sutures between columnals, heteromorphic; proximal section of low columnals with epifacet slightly wider on nodals, noditaxis N1.

REMARKS. This species is distinguished from *F. enidae* by its smooth plates, longer radials and greater number of secundibrachs per arm.

**Frankocrinus enidae** sp. nov.
(Figs 24, 25)

MATERIAL. HOLOTYPE: NMVP108571. PARATYPE: NMVP108622 from NMVPL252.

DIAGNOSIS. Crown with external finely punctate ornament. Radials smaller relative to cup size than in other hexacrinitids. Arms 20, fixed in cup up to 2nd secundibrach, uniserial, pinnulate, of cuneate brachials, with strongly crenulate interbrachial sutures. Fixed arms separated by depressed areas occupied by single large interprimibrach. Stem circular in section, with crenulate attachment suture.

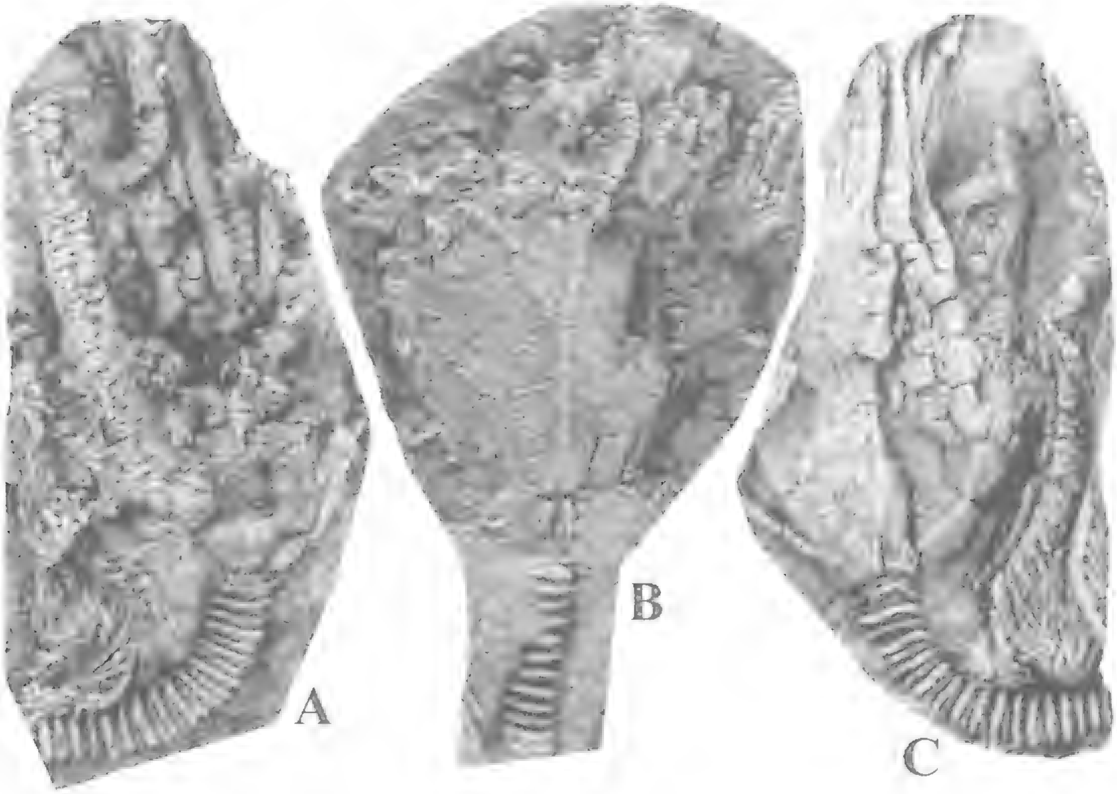



FIG. 26. *Alisocrinus lineatus* sp. nov. incomplete crowns from NMVPL300. A, C, part and counterpart of paratype NMVP109791, ×3. B, C ray view of holotype NMVP110632, ×3.

DESCRIPTION. Crown estimated to be 35mm long, conical. Cup high conical, consisting of basals, radials and primanal, with ray ridges low broad indistinct. Basals 3, equal, hexagonal, symmetrically proximal to A, C and D radials, each with vertical median ridge. Radials 5, only slightly longer than wide, with broad low ridges continuing from basals; radial facet about 2/3 radial width, declivate, subsemicircular. Primanal same size as radials, smooth, without facet. Arms 20, uniserial, with deep groove on inner side; 2nd primibrach and secundibrach axillary, pentagonal; tertibrachs cuneate, almost circular in section, pinnulate, with large well developed facet for attachment of pinnule; pinnules one per brachial, alternating from side to side along each arm, long, well spaced. Tegmen of small irregular polygonal plates. Stem circular in section, with strongly crenulate sutures between columnals, noditaxis N1 with lateral flange at midlength of latus slightly wider on nodals, with columnals increasing gradually in length distally, with lateral midlength flange occupying only small part of length, with large circular central lumen.

REMARKS. This species is distinguished from *F. holmesi* under that species above. The basal circlet crushed up into the calyx of the holotype makes determination of proportions impossible and has broken and concealed the primanal (at 5 o'clock Fig. 24D) masking features of the posterior of the cup. Ornament is a little more linear on the paratype but nevertheless it is still punctate as in the holotype. Crown length or shape is not available due to presevational features.

Suborder GLYPTOCRININA Moore, 1952
Superfamily MELOCRINITOIDEA d'Orbigny, 1852
Family MELOCRINITIDAE d'Orbigny, 1852

The evolutionary lineage outlined by Kirk (1929), Ubaghs (1958) and Brower (1976) beginning in the Ordovician Glyptocrinidae, through *Alisocrinus*, *Ctenocrinus*, *Melocrinites* and to

*Trichotocrinus* in the Middle Devonian is accepted, as are the generic concepts of those authors. However, Kesling's (1964) comment that the concepts of several type species are so poorly understood that he considered *Ctenocrinus* among other genera to be synonymous with *Melocrinites* is equally applicable to the myriad of species assigned to these genera. More than 40 specific names are currently included in *Ctenocrinus* and doubtless this is a figure inflated by intraspecific variation and preservation and failure on the part of several authors to recognise growth series. It is not the aim of this paper to assess these essentially European and North American taxa; I have illustrated many specimens of this very common element of the Victorian fauna to facilitate future species level revisions of the family. Assignment to established species from the Northern Hemisphere is a deliberate effort to avoid introducing new names into an already overcrowded arena. These are the closest known species available but future work on the status of known species could change the concept of any or all of the 3 and could necessitate reassignment of the Australian material. My assignments are made by comparisons with published illustrations, not all of them photographic, which may require reassessment.

### **Alisocrinus** Kirk, 1929

TYPE SPECIES. *Mariacrinus warreni* Ringueberg, 1888 from the Middle Silurian of New York; by original designation.

DIAGNOSIS. See Ubaghs (1978).

### **Alisocrinus lineatus** sp. nov. (Fig. 26)

ETYMOLOGY. Latin *lineatus*, linear, for the ornament.

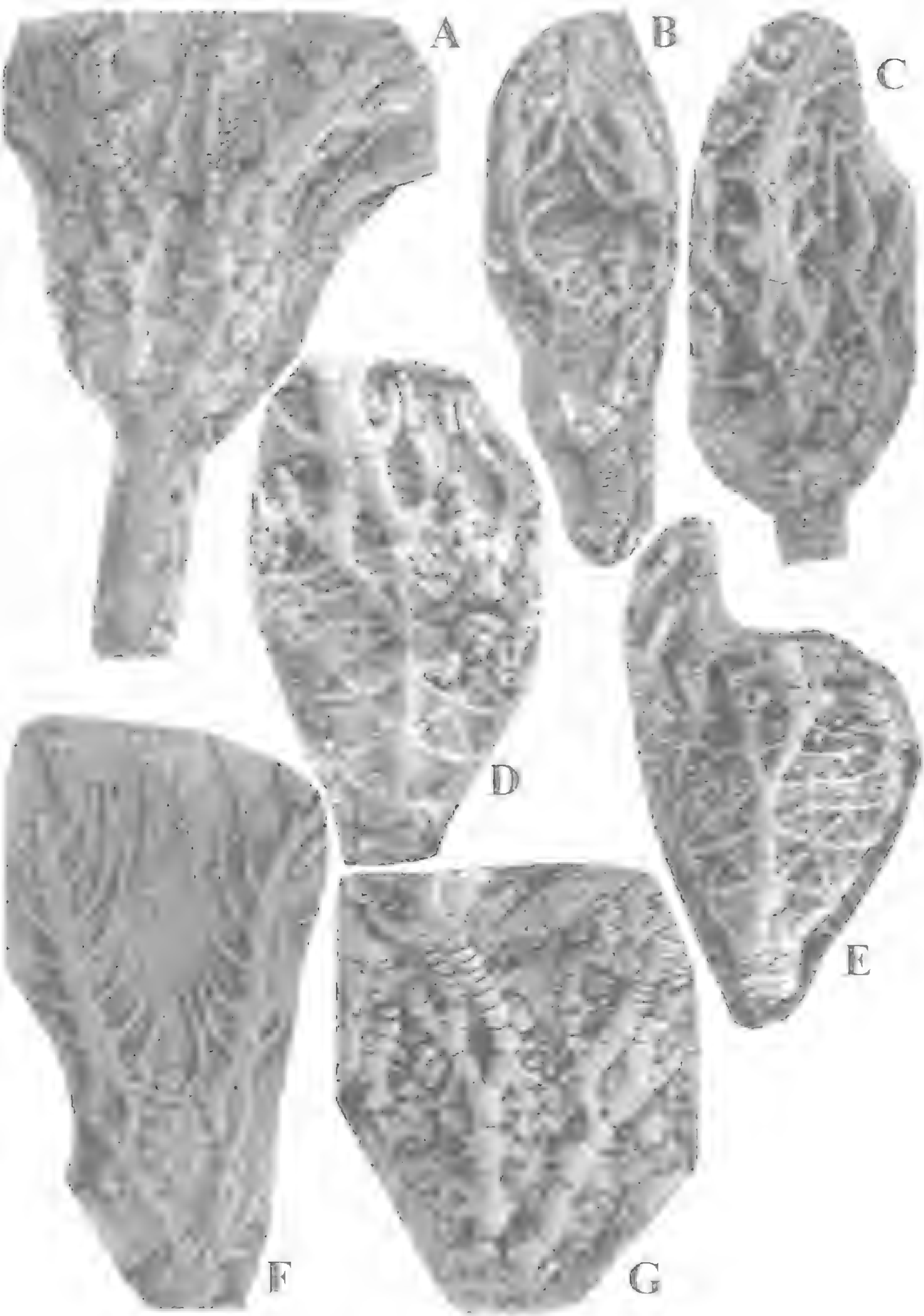
MATERIAL. HOLOTYPE: NMVP110632. PARATYPE: NMVP109791 from NMVPL300.

DIAGNOSIS. Cup plate ornament of narrow low ray ridges and fine radial ridges on a background of fine tubercles. Arms fixed in cup up to 1st tertibrach, 4 per ray, uniserial, of cuneate brachials; 2nd primibrach and 3rd secundibrach axillary.

DESCRIPTION. Crown up to 35mm long, subcylindrical. Cup high, conical, up to 15mm long; cup plates large, thin, with ornament of radial ridges (including ray ridges) and fine raised incomplete and irregular comarginal growth bands (so incomplete as to be simply a fine tuberculate ornament on most plates). Basals 4, with 3 of them pentagonal, with one larger and hexagonal, with proximal margin as distinct rim to stem attachment, with fine continuous ray ridges diverging distally from midpoint of base to cross 2 distal sides at right angles, with extra central vertical ridge bisecting CD interray on posterior basal. Radials 5, heptagonal, largest plates in cup, with inverted Y-shaped ray ridges continuing from basals and onto 1st primibrach, with secondary radiating ridges horizontally onto adjacent radials and sloping onto 1st interprimibrachs, all ridges at right angles to sutures. Primanal heptagonal, resting on shoulders of 2 adjacent radials, supporting 3 plates above, with 7 fine radial ridges radiating from centre to middle of each side and beyond to contiguous plates. Anal interray wider than others, with large polygonal plates decreasing in size upwards (arrangement unclear on only available specimen). First primibrach hexagonal, with broad low median ray ridge running in vertical line, with fine ridges running diagonally to other 4 lateral sutured margins; 2nd primibrach axillary, heptagonal, with median ray ridge in Y-shape to enter 2 arms. Secundibrachs fixed in cup, hexagonal, as large as primibrachs, 3rd axillary. Arms 20, uniserial, free above 2nd division, tapering gently, with longitudinal grooves on outer side of arms; free brachials cuneate, with pinnules one per brachial alternating from side to side along each arm. Interprimibrachs numerous, not depressed, with single large plate in contact with 2 radials and 1st primibrachs and supporting next row of 2 interprimibrachs, with plates in subsequent rows becoming smaller and less regularly arranged; intersecundibrachs tiny by comparison, few in number, depressed, polygonal, irregularly arranged. Tegmen unknown. Stem circular, heteromorphic, with wider epifacet on nodals but all columnals of about same height.

REMARKS. This species is distinguished from the genotype by the finer ray ridges and 3 rather than 2 secundibrachs. It is separated from the other species of the genus by its generally finer plate ornament and 3 rather than 2 secundibrachs.

FIG. 27. *Ctenocrinus paucidactylus* (Hall, 1859), all crowns in lateral view from NMVPL229 except C from NMVPL252. A, NMVP149377, ×3.5 . B, NMVP109158, ×2.5. C, NMVP108583, ×3. D, NMVP110646, ×2. E, NMVP108961, ×3. F, NMVP109154, ×1.5. G, NMVP149378, ×2.


A
B
C
D
E
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G

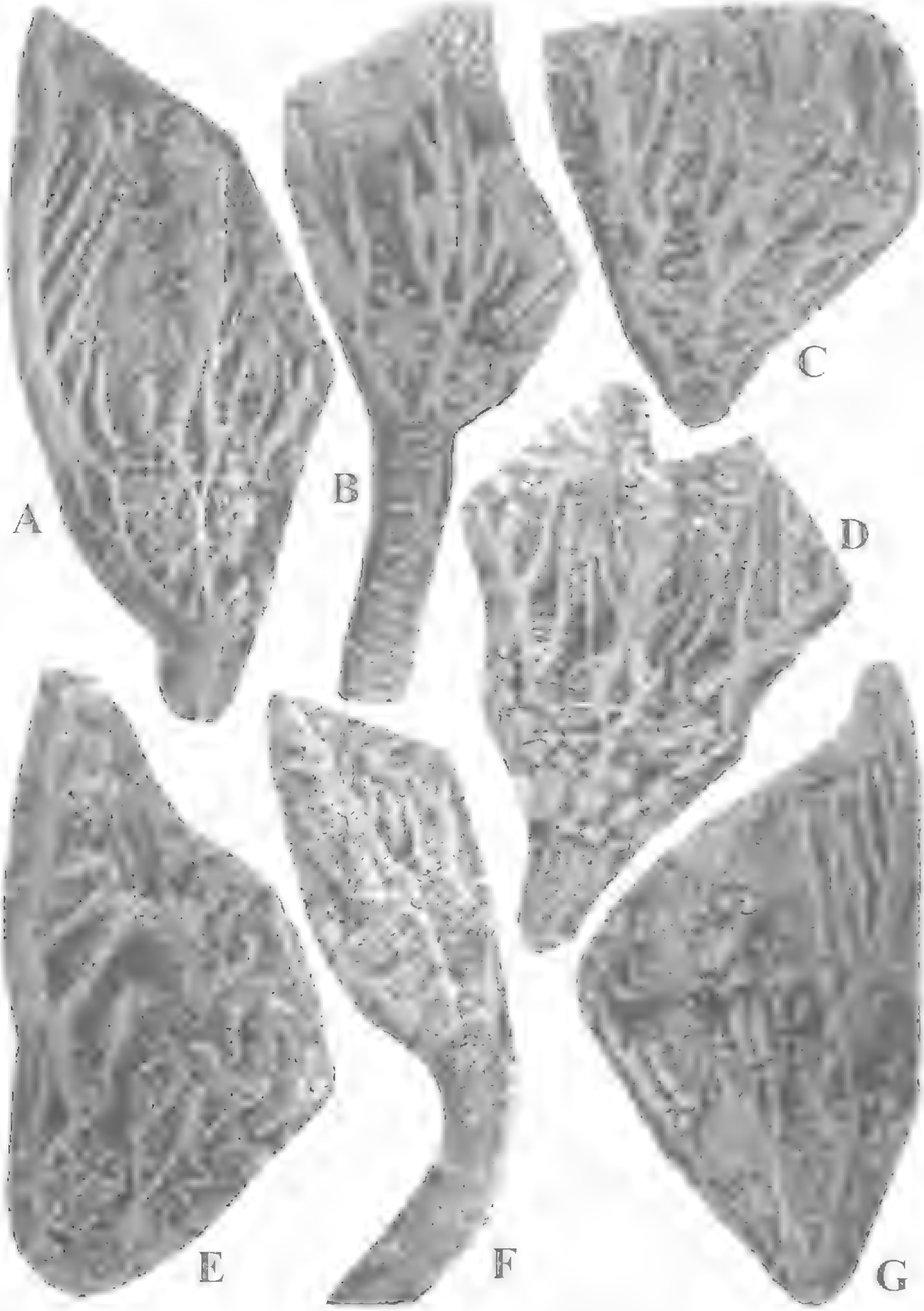



FIG. 28. *Ctenocrinus paucidactylus* (Hall, 1859), all incomplete crowns in lateral view from NMVPL229. A, NMVP149379, ×3. B, NMVP108968, ×4. C, NMVP149380, ×2. D, NMVP109165, ×2. E, NMVP100165, ×2.5. F, NMVP109117, ×2. G, NMVP149381, ×2.

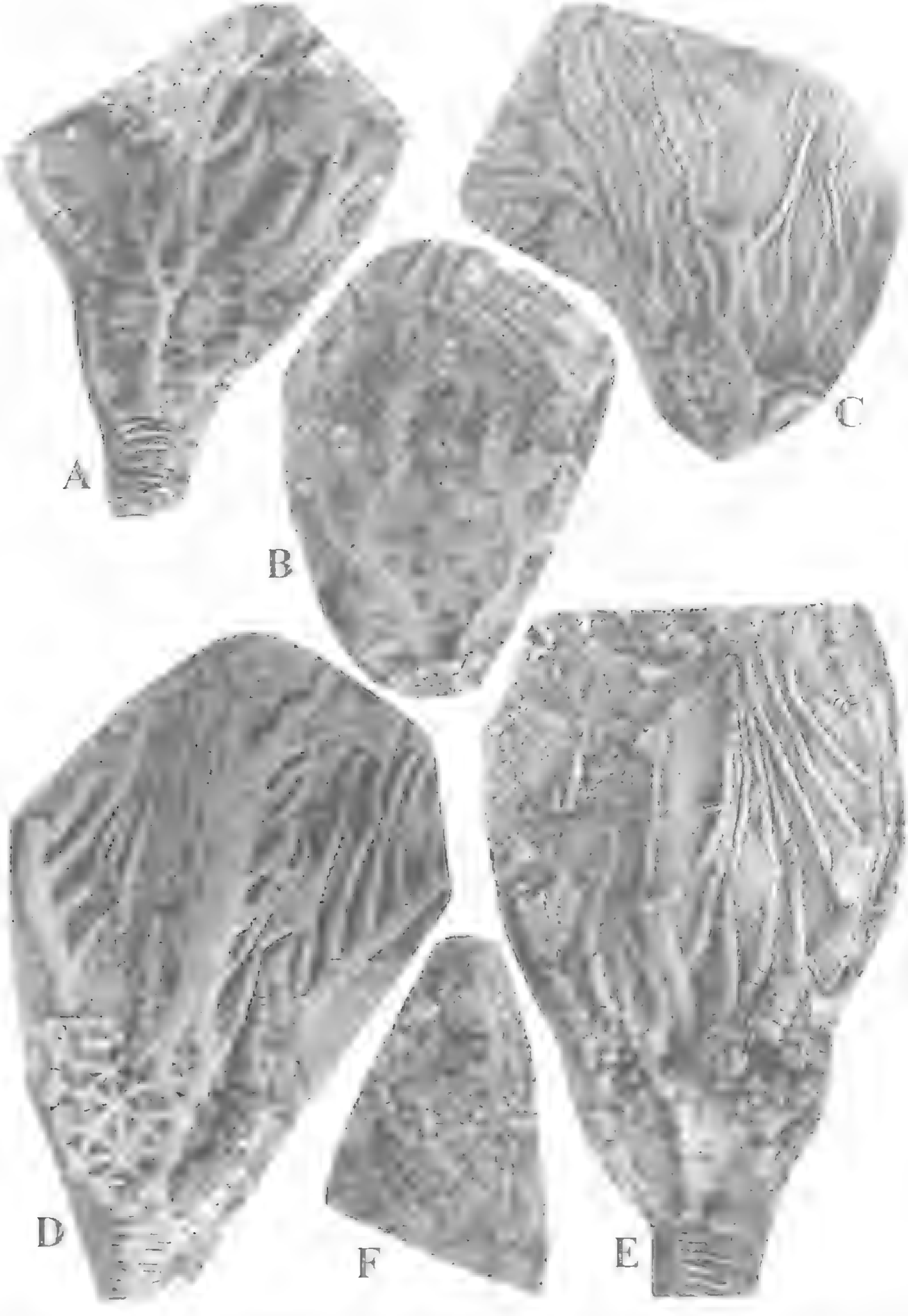



FIG. 29. *Ctenocrinus paucidactylus* (Hall, 1859), all incomplete crowns in lateral view from NMVPL229 except C from NMVPL252. A, NMVP109111, ×2.5. B, NMVP100168, ×2.5. C, NMVP108596, ×2.5. D, NMVP108610, ×2.5. E, NMVP108956, ×2.5. F, NMVP149382, ×2.5.

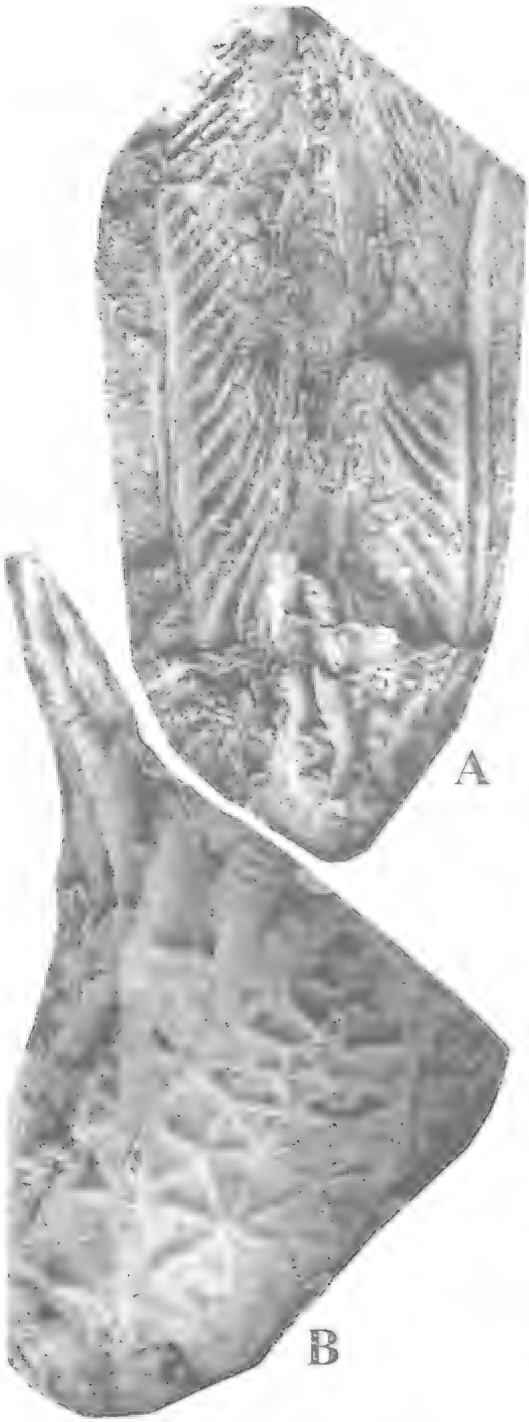



FIG. 30. *Ctenocrinus paucidactylus* (Hall, 1859), both from Locality 25, N of Heathcote (Talent, 1965). A, large set of arms with partial upper cup NMVP149356, ×1. B, large partial cup and arms NMVP149383, ×1.5.

### **Ctenocrinus** Bronn, 1840

TYPE SPECIES. *Ctenocrinus typus* Bronn, 1840 from the Lower Devonian of Germany.

REMARKS. In light of the discussion under the family heading above I have not attempted to diagnose these species erected last century but have attempted to illustrate their features in the descriptions provided below. The description of the first species applies to all 3 in most features so descriptions of succeeding species are provided only where they differ from that of *C. paucidactylus*.

The species to which the Australian material is assigned belong to what Brower (1976) termed primitive *Ctenocrinus*.

### **Ctenocrinus paucidactylus** (Hall, 1859)
(Figs 27-30, 31A-E)

MATERIAL. NMVP100165, 100168, 108685, 108956, 108961, 108964, 108968, 109111, 109117, 109127, 109154, 109158, 109165, 109168, 110646, 149377-149382 from NMVPL229; NMVP108583, 108596, 108610, 110636 from NMVPL252; NMVP149356 and 149383 from locality 25 in the Mt Ida Formation of Talent (1965, fig. 1).

DESCRIPTION. Crown up to 170mm long (NMVP148625), averaging 60-80mm long at NMVPL229 and 252. Cup high conical; surface of plates with strong radial ornament of narrow strongly convex ridges of uniform width throughout except for ray ridges being wider and more prominent than the rest. Basals 4, with interplate sutures at A, C, D and E rays, at least 4mm long. Radials 5, large, in contact laterally, 9mm long and 8mm wide at the widest point 3mm from the top, with 7 sides including horizontal distal margin and broadly chevron shaped proximal margin. First primibrach hexagonal, with horizontal proximal and distal margins, 7mm long by 6mm at greatest width near midlength. Second primibrach axillary, variously hexagonal or heptagonal, with strong dividing median ray ridge and markedly thinner and weaker radiating ridges laterally; 2nd secundibrach axillary, giving rise to larger inner arm trunk and smaller outer ramule. Arms 10, up to 4 times as long as cup, fixed in cup to about 3rd or 4th tertibrach; 2 arm trunks per ray laterally sutured into pseudobiserial structure, essentially a single arm, sharing a single groove down the inner side, with every 6-8th tertibrach axillary, 5-sided, with upper obtuse angle about midwidth of arm, branching off long uniserial pinnulate ramules at each axillary. Interprimibrachs

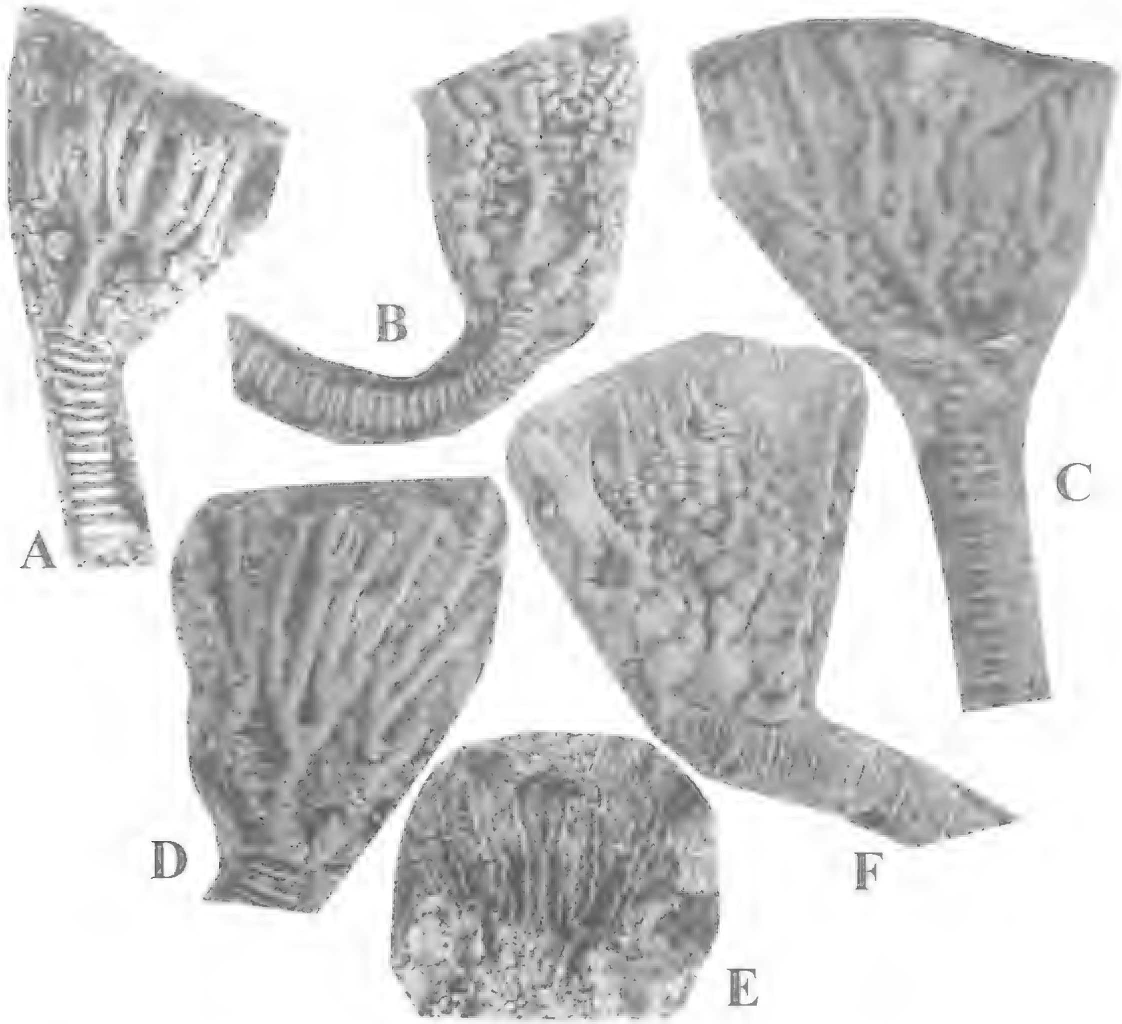



FIG. 31. A-E, *Ctenocrinus paucidactylus* (Hall, 1859), juvenile crowns all from NMVPL229 except C from NMVPL252. A, NMVP109127, ×3.5. B, NMVP108964, ×4.5. C, NMVP110636, ×3.5. D,E, exterior and inner side of arms, respectively NMVP108685, ×5. F, *Ctenocrinus signatus* Follmann, 1887, crown NMVP109152 from NMVPL229, ×2.

numerous, with large proximal one resting on shoulders of 2 radials, with striking ornament of high narrow radial ridges of uniform width (not expanded at centre of plate); 2nd row of 2 plates except in CD interray with 3 in 2nd row; subsequent rows less regular, of smaller plates, merging into the tegmen just above the fixed 2nd secundibrach. Intersecundibrachs 2, small, pentagonal, enclosed by large central arms in each ray, with central tubercle and weak radial ridges. Intertertibrachs between larger inner arm and first outer arm very small, irregular, up to 8, with central prominence on each and lateral ridges running between the inner and outer arms. Stem circular in section, heteromorphic, higher and wider nodals alternating with internodals.

**Ctenocrinus stellifer** Follman, 1887
(Figs 32-34)

MATERIAL. Syntypes of Follmann (1887, pl. 2, fig. 2, 2a,b) in the Bonn University Museum. Australian material assigned NMVP100175, 100188, 108584, 108589, 108597, 108603, 108658, 108684, 149384-149386 all from NMVPL252; NMVP149346 from NMVPL1990; NMVP149357 from NMVPL1841.

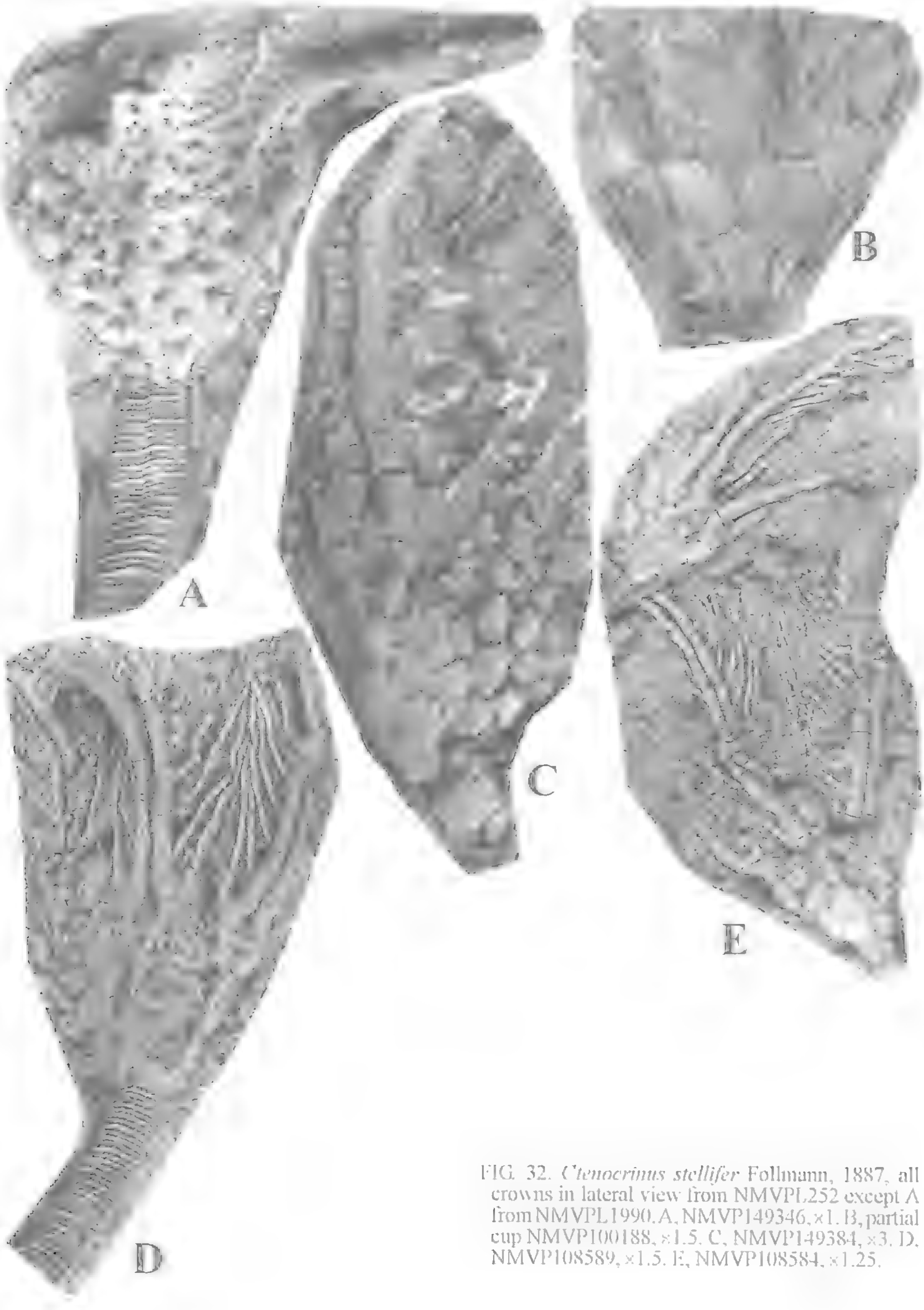


FIG. 32. *Ctenocrinus stellifer* Follmann, 1887, all crowns in lateral view from NMVPL252 except A from NMVPL1990. A, NMVP149346, ×1. B, partial cup NMVP100188, ×1.5. C, NMVP149384, ×3. D, NMVP108589, ×1.5. E, NMVP108584, ×1.25.

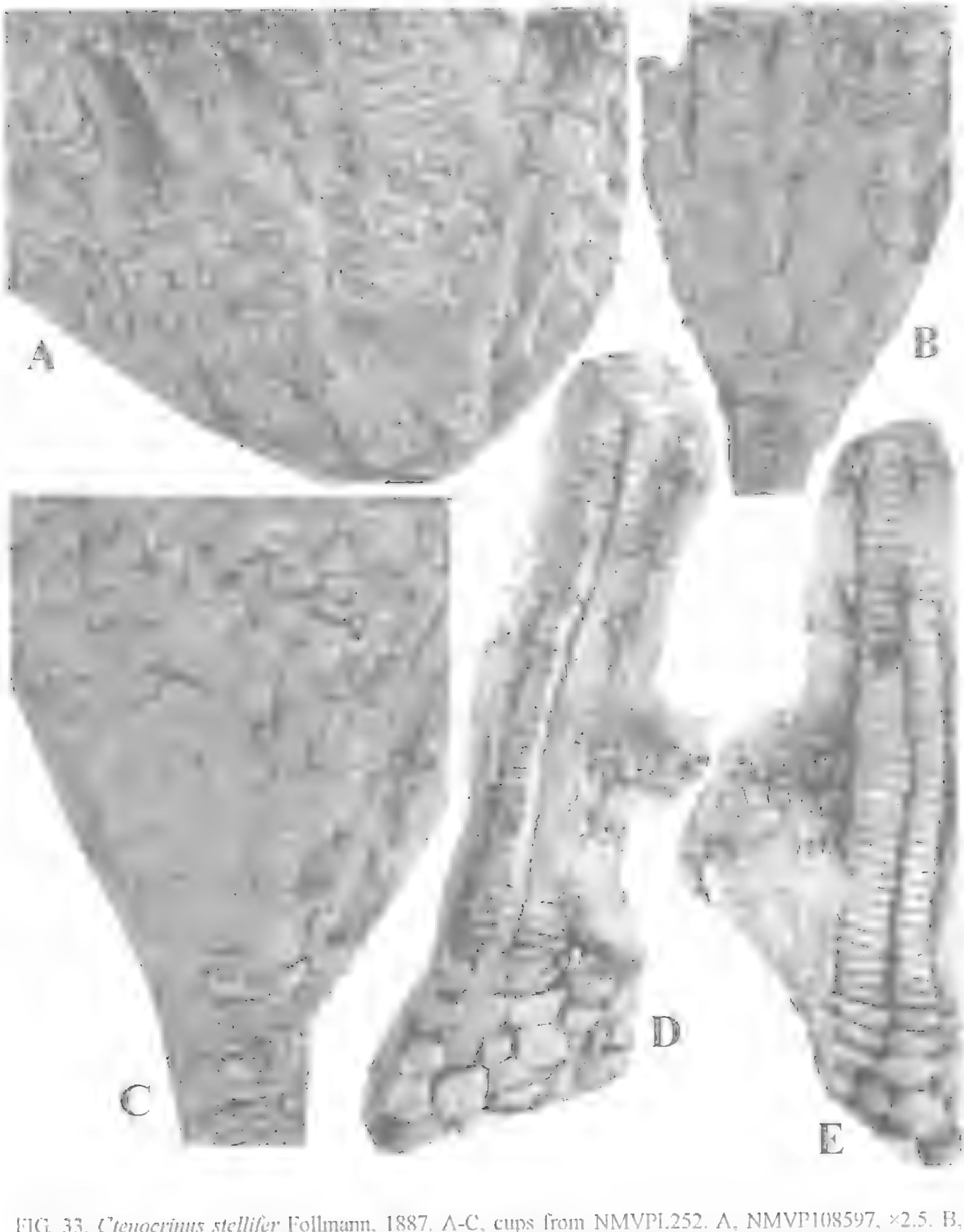



FIG. 33. *Ctenocrinus stellifer* Follmann, 1887. A-C, cups from NMVPL252. A, NMVP108597, ×2.5. B, NMVP108603, ×2. C, NMVP100175, ×2. D, interior and exterior of an arm NMVP149357 from NMVPL1841, ×1.5.

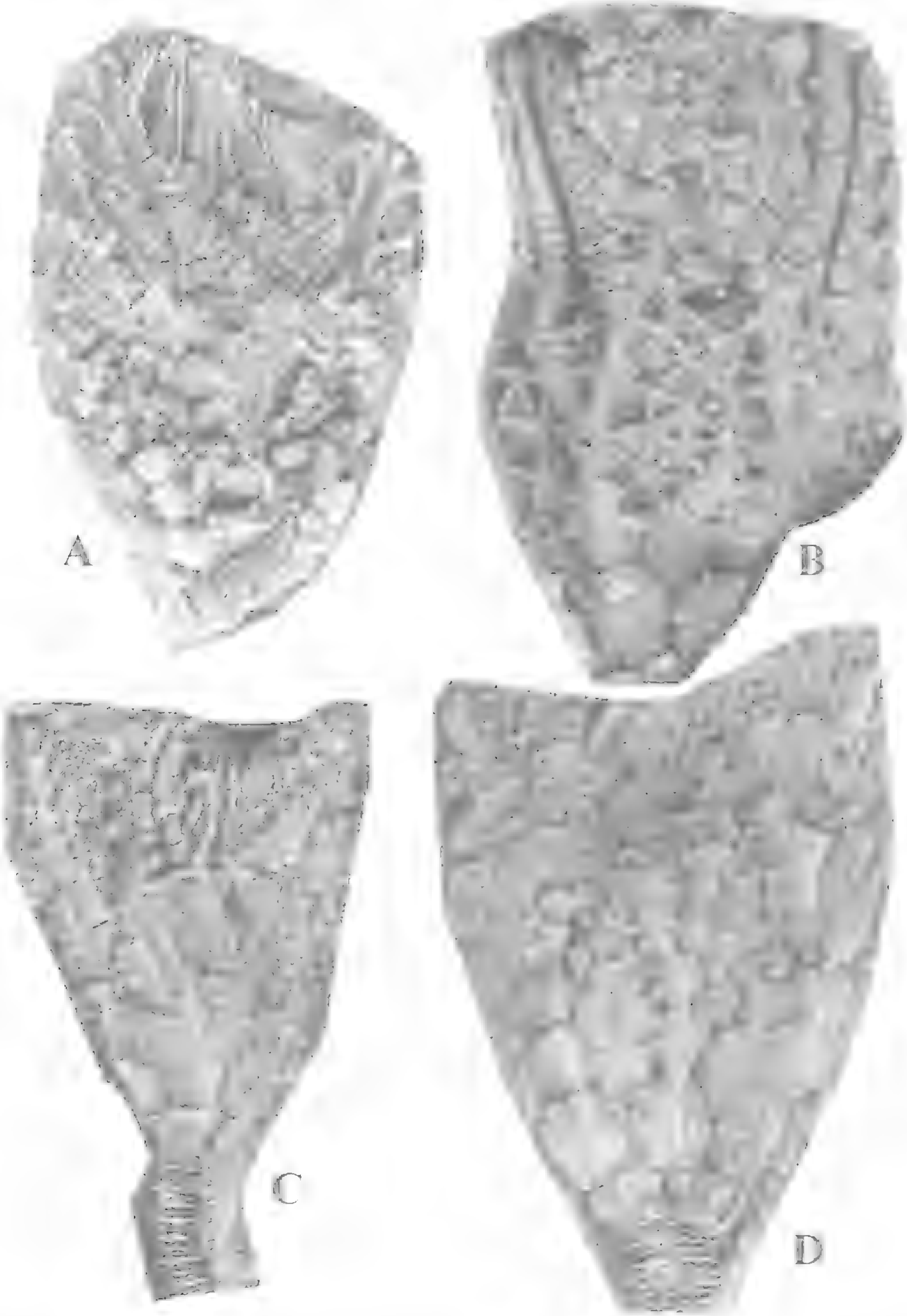



FIG. 34. *Ctenocrinus stellifer* Follmann, 1887, all crowns in lateral view (A interior view) from NMVPL252. A, NMVP149385, ×4. B, NMVP149386, ×3. C, NMVP108684, ×2. D, NMVP108658, ×3.

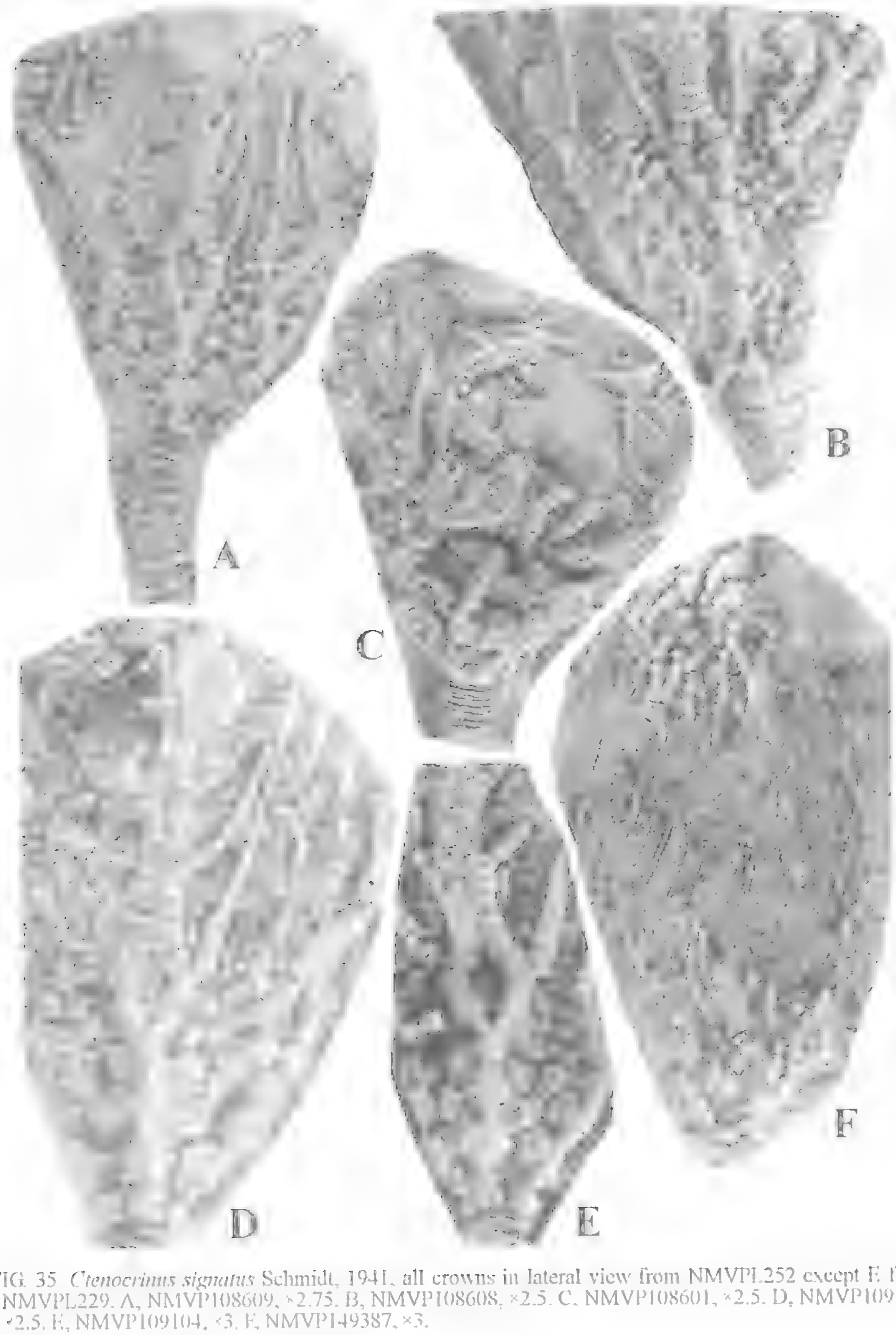



FIG. 35. *Ctenocrinus signatus* Schmidt, 1941, all crowns in lateral view from NMVPL252 except E from NMVPL229. A, NMVP108609, ×2.75. B, NMVP108608, ×2.5. C, NMVP108601, ×2.5. D, NMVP109167, ×2.5. E, NMVP109104, ×3. F, NMVP149387, ×3.

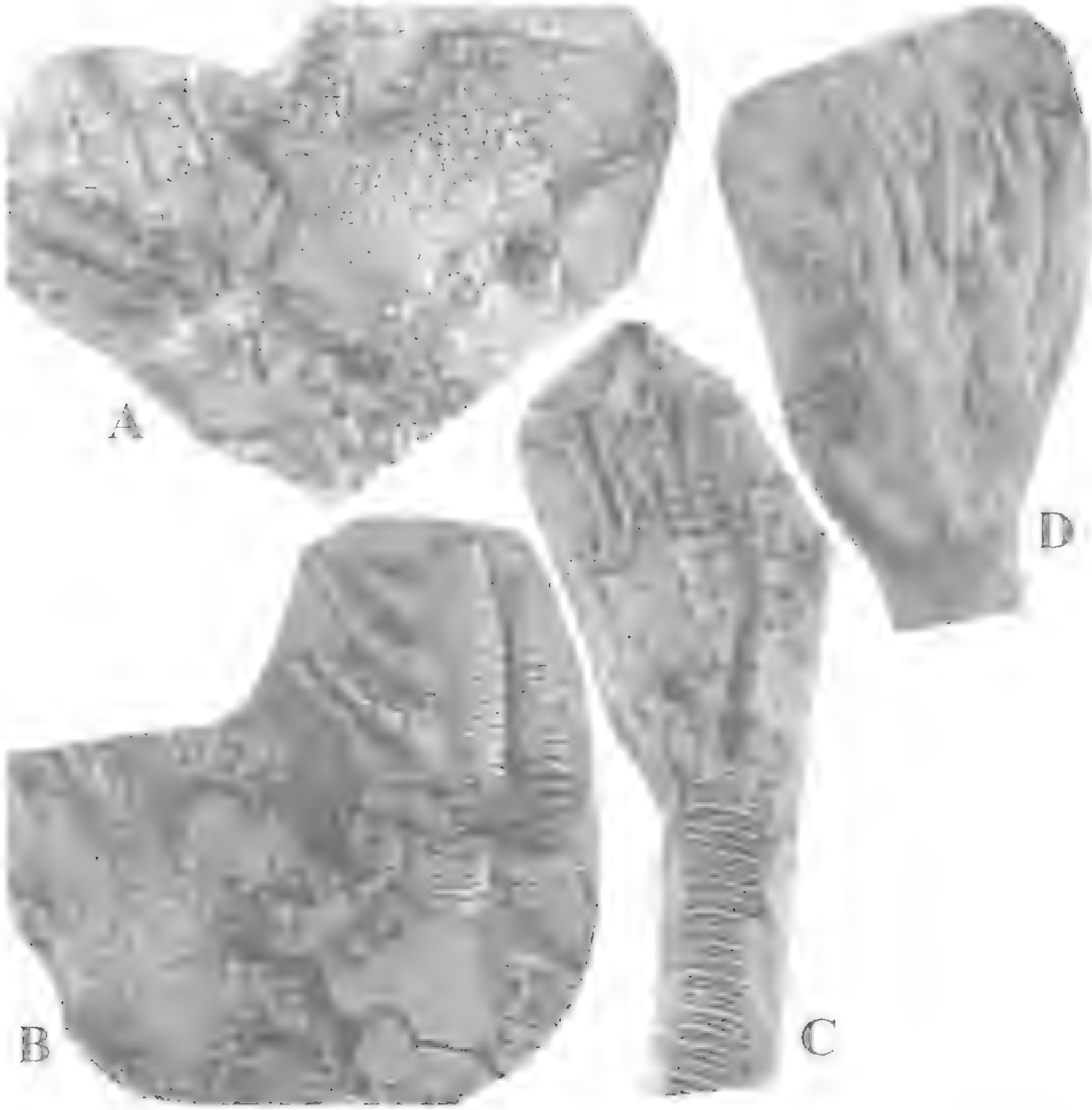



FIG. 36. *Ctenocrinus* sp. all from NMVP1924. A,B, part and counterpart of tegmen with some arm fragments NMVP109756, ×3. C, crown NMVP109750, ×2. D, crown NMVP109222, ×4.

DESCRIPTION. Crown up to 80mm long. Otherwise as for *C. paucidactylus* except: 1, plate ornament including the ray ridges, is greatly reduced on proximal parts of the cup; 2, tertiary ridges occur especially in the proximal plates of the cup parallel to the radial ornament; 3, 1st intersecundibrach with radial ridges running onto adjacent plates and producing distinctive 5-rayed star not evident in other Australian species; 4, ramules with axillary brachials slightly longer on outer side but otherwise no modification to arm trunk.

REMARKS. Reduced ornament on the proximal cup is clear on Schmidt's (1941, pl. 8, fig.4b) figure. Schmidt (1941, fig. 17) illustrated the tertiary ridges parallel to the radial ridges on proximal plates and the distinctive radial ornament of the 1st intersecundibrach. Follmann (1887, fig. 2, 2a,b) showed the last mentioned feature (fig. 2a) and the laterally longer axillary

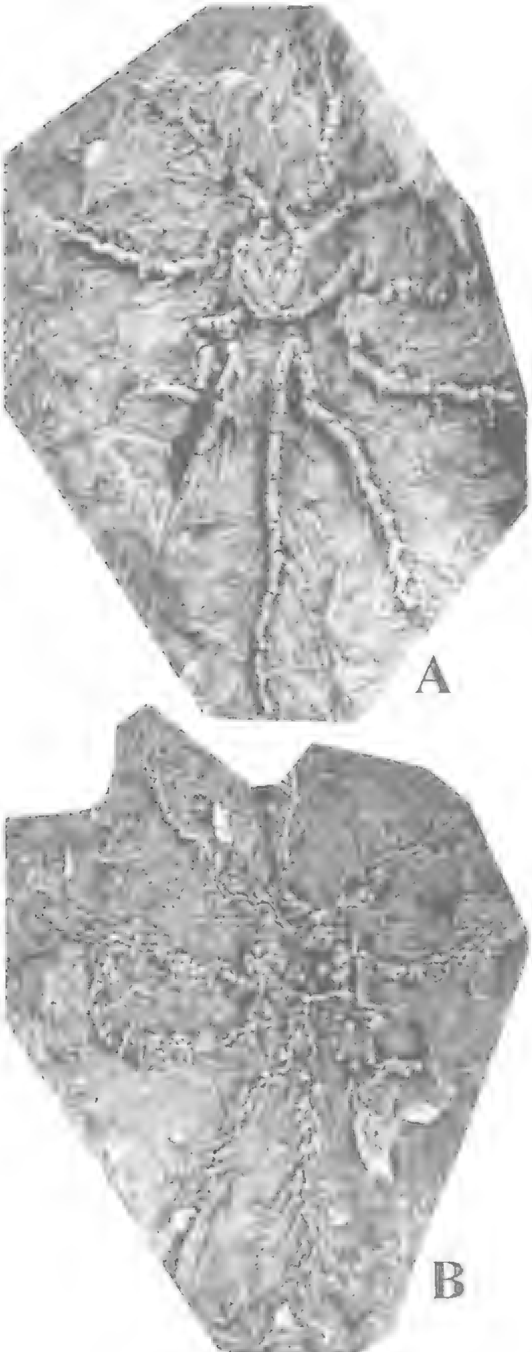



FIG. 37. *Hapalocrinus? victoriae* Bather, 1897, part and counterpart of splayed holotype crown NMVP386, from Yarra Improvement works near Prince's Bridge, ×2.

brachials in the arm trunks; however, he showed a ramule arising about every 3rd or 4th brachial whereas the Australian species has upto 9 nonaxillary brachials in a row, averaging 6-8. Assignment to *stellifer* is made with slight reservation but it is a better match than with any other known species.

**Ctenocrinus signatus** Schmidt, 1941
(Figs 31F, 35)

MATERIAL. HOLOTYPE: in the Bonn Museum (Schmidt, 1941:73, fig 18a). Australian material assigned NMVP108601, 108608, 108609, 109167, 149387 from NMVPL252 and NMVP109104, 109152 from NMVPL229.

DESCRIPTION. Crown up to 70mm long. Otherwise as for *C. paucidactylus* except in relation to plate ornament as discussed below and in the branching of ramules where the axillaries in the arm trunks are quite asymmetrical, the facet for the ramule being much smaller and more lateral than that for the continuing central arm.

REMARKS. This species assignment is made principally on plate ornamentation which consists of a raised flat-topped central tubercle that is expanded laterally to occupy about half the plate area and from which the radial ridges radiate only a short distance so producing a stellate ornament. This ornament is unlike that of *C. paucidactylus* where the radial ridges maintain a uniform width even across the centre of the plate and even though it is subdued in some specimens (Fig. 35D) it is still much more pronounced than in *C. rhenanus* and it lacks tertiary ridges also.

**Ctenocrinus** sp.
(Fig. 36)

MATERIAL. NMVP109222, 109750, 109756 from NMVPL1924.

DESCRIPTION. As for *C. paucidactylus* except 1, plate ornament is virtually absent, although one specimen (Fig. 36D) retains a very subdued radial ornament on basals, radials and primibrachs. 2, the tegmen consists of a very large number of tiny polygonal plates, with a small diameter anal tube (broken base only on this specimen). 3, largest specimen with a fringe of tiny plates between bases of ramules adjacent to arm trunks. 4, brachials forming ramules with proximal and distal margins parallel in exterior view but cuneate in interior view.

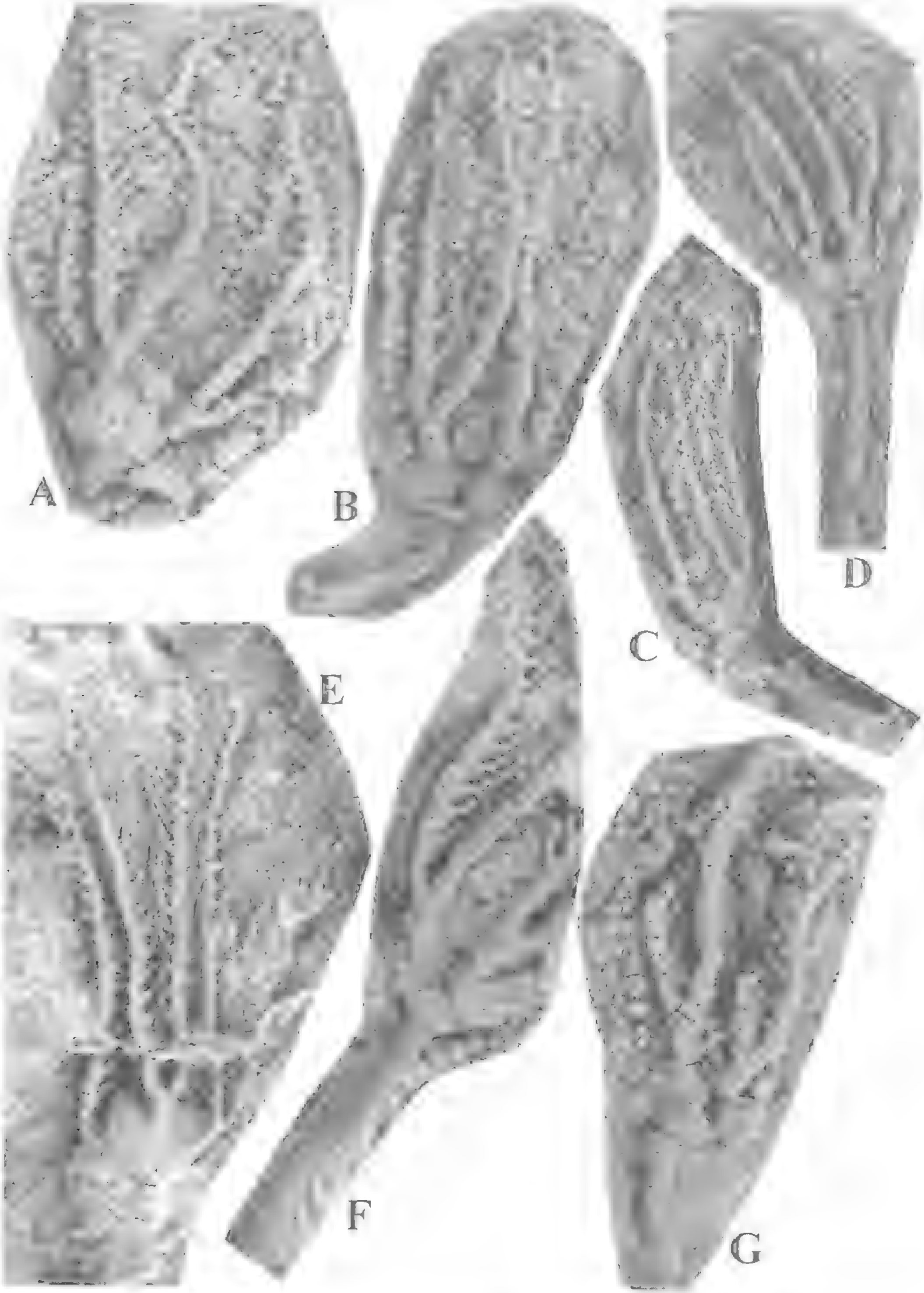



FIG. 38. *Clematocrinus perforatus* sp. nov., all crowns in lateral view from NMVPL300. A, NMVP109816, ×4.5. B, NMVP149388, ×4. C, NMVP109824, ×2. D, NMVP109821, ×4. E, NMVP109782, ×5. F, NMVP109785, ×5. G, NMVP109811, ×5.

REMARKS. This material with reduced plate ornament could be placed with *C. stellifer* from NMVPL252 but features listed above, in particular features of the mature arm and lack of ornament make such identification doubtful and it is best left in open nomenclature.

Superfamily PLATYCRINITOIDEA Austin & Austin, 1842
Family HAPALOCRINIDAE Jaekel, 1895

**Hapalocrinus** Jaekel, 1895

TYPE SPECIES. *Hapalocrinus elegans* Jaekel, 1895 from the Lower Devonian of Germany.

**Hapalocrinus(?) victoriae** Bather, 1897
(Fig. 37)

MATERIAL. NMVP386a and b from the Yarra Improvement Works near Prince's Bridge, Melbourne, in the Ludlovian Melbourne Formation.

DESCRIPTION. Crown splayed; form of cup uncertain, basal circlet not discernible. Radials 5, 7-sided (one being radial facet), smooth, widest at distal shoulders. Arms 10, up to 15mm long, with 3 primibrachs, 3rd axillary, uniserial, with well-developed facets for pinnule attachment giving zigzag appearance to arm; pinnules 1 per brachial alternating along each arm, widely separated, long (up to 5mm) and thin, with 4-6 long pinnulars; brachials rectangular, about twice as high as wide, with wide strongly zigzag groove on inner surface.

REMARKS. The detail of this specimen is not certain as was acknowledged by Bather (1897: 337, footnote 3) when he said he could not vouch for each line in his drawing. However, I agree with his general conclusions and only the nature of the basal circlet described by Bather is not readily apparent to me. Since so few features are available a separate diagnosis is not provided; the species is principally distinguished by its long brachials in the arms and is deliberately isolated on the type because of the difficulty of comparing other material with it.

Ausich (1986b) discussed this species in relation to Ubaghs' (1978b) tentative extension of the range of *Clematocrinus* to include Australia. I agree with Ausich's (1986b) conclusion supporting separation of the 2 genera and retain *victoriae* in *Hapalocrinus* based principally on the 3 primibrachs.

Bather (1897) noted that the counterpart of the type specimen was lost but part and counterpart have been reunited in the Museum of Victoria collection.

FIG. 39. *Clematocrinus perforatus* sp. nov., crown NMVP100185 from NMVPL252, ×3.

**Clematocrinus** Jaekel, 1898

TYPE SPECIES. *Actinocrinites? retiarius* Phillips in Murchison, 1839 from the Wenlock of England; by monotypy.

DIAGNOSIS. See Ausich, 1986b: 894.

REMARKS. Ubaghs (1978b:512) tentatively extended the distribution of this genus to include North America and Australia but as noted above there are no published records in Australia and *H. victoriae* cannot be considered a member of this genus. Ubaghs (1978b:518) suggested that Chapman's (1903) *Helicocrinus*, although of uncertain placement, might be a hapalocrinid but that genus is best isolated on the type specimen with features as noted below.

**Clematocrinus perforatus** sp. nov.
(Figs 38-40)

ETYMOLOGY. Latin *per-*, through and *foramen*, hole; referring to the stem appearing perforate.

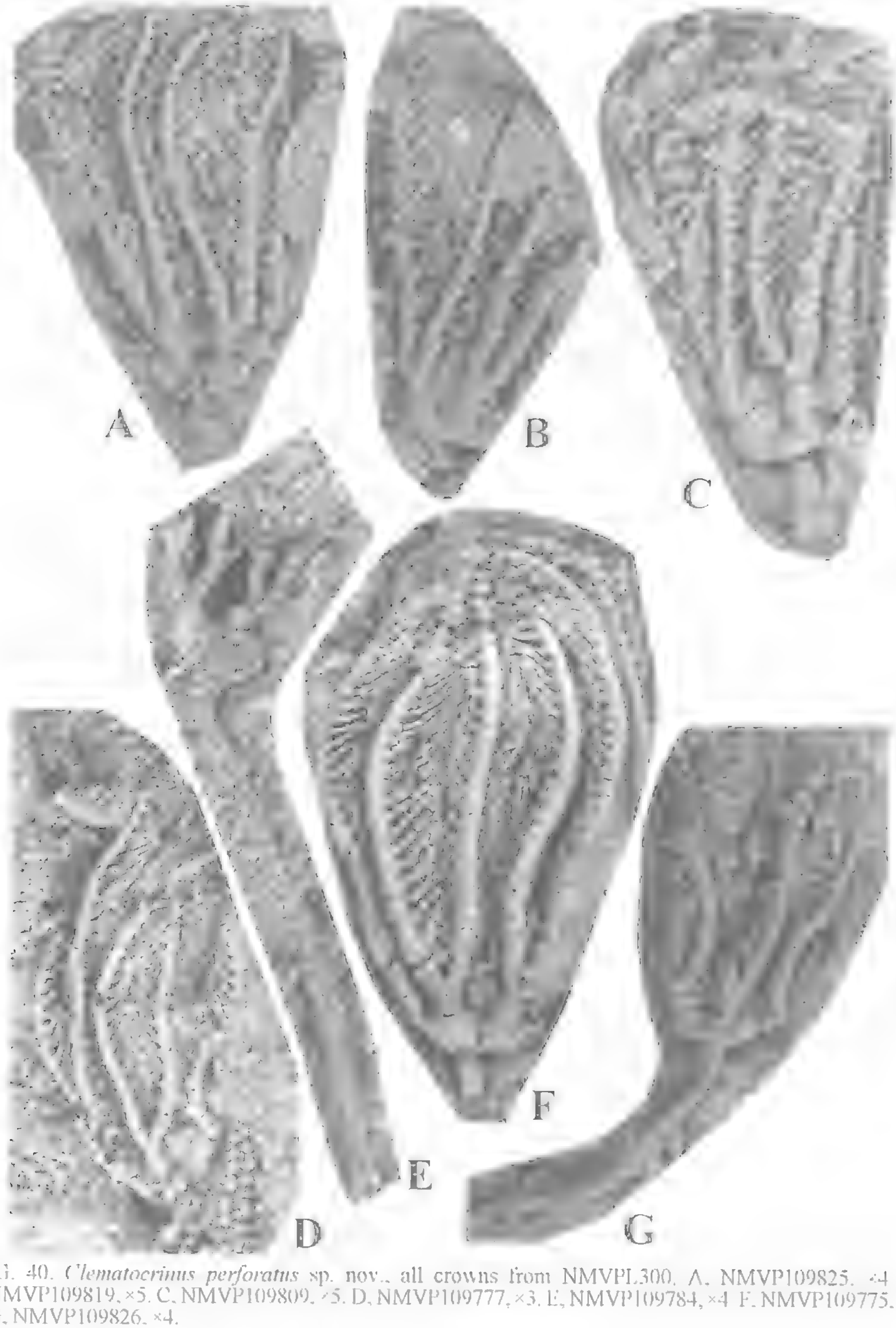



FIG. 40. *Clematocrinus perforatus* sp. nov., all crowns from NMVPL300. A, NMVP109825, ×4. B, NMVP109819, ×5. C, NMVP109809, ×5. D, NMVP109777, ×3. E, NMVP109784, ×4. F, NMVP109775, ×3. G, NMVP109826, ×4.

MATERIAL. HOLOTYPE: NMVP109782. PARATYPES: NMVP109775, 109777, 109782, 109784, 109785, 109805, 109809, 109811, 109816, 109819, 109821, 109824, 109825, 109826, 110624, 110627, 110628, 110629, 110631, 110633, 110642, 149388 all from NMVPL300; NMVP100185 from NMVPL252.

DIAGNOSIS. Cup bowl-shaped. Basal circlet apparently fused. Posterior interray with vertical anal tube of large polygonal plates. Arms 10, uniserial, of low subquadrate (in lateral view) cuneate brachials. Stem noncirriferous, with crenulate intercolumnal sutures, with columnals becoming longer and epifacet breaking up into an annulus of tubercles distally.

DESCRIPTION. Crown elliptical, 32mm long. Cup low bowl-shaped, about 5mm high, radially symmetrical except in posterior interray, without basal concavity. Cup plates smooth, thin, convex. Basals apparently fused into pentagonal unit, short in lateral view, with circular crenulate stem facet occupying central 1/2-2/3. Radials 5, forming complete circlet, largest plates in cup, occupying about 1/2 cup length, hexagonal, convex with distal corners depressed. Radial facet horizontal, just over half radial width. Arms 10, free distal to primaxil, uniserial; 1st primibrach subquadrate, with convex raised central part and depressed lateral flanges; 2nd primibrach pentagonal, axillary, fixed in cup, with depressed lateral flanges; brachials variable in proportions but usually wider than long, subquadrate proximally, rapidly becoming cuneate distally; pinnules 1 per brachial, alternating along each arm, long, becoming more slender distally, of long pinnulars (4-6 per pinnule). Proximal interprimibrach large, hexagonal, resting on depressed shoulders of adjacent radials, only interbrachial in cup; CD interray with row of 3 anal plates resting on shoulders of C and D radials, with interbrachials protruberant in elongate convex bulge; primanal central, pentagonal, smaller than proximal interbrachial of other interrays, flanked by smaller anal sac plates in contact with primibrachs. Tegmen with short stout anal tube at posterior. Stem circular in section, heteromorphic; proximally with alternating nodals and internodals of similar length but with epifacets or annular flange at midlength of latus being wider on the nodals; distally with uniform columnals, each with the epifacet at midlength of latus broken up into a circlet of small nodes; intercolumnal articulations symplexial, with culmina from one columnal not fitting neatly into opposing crenellae on next columnal so producing the effect of two adjacent circlets of pores around stem.

REMARKS. This species is distinguished within the genus by its distinctive stem, narrow radial facets, uniserial arms and posterior anal tube. Australian species do not closely resemble any of the other species and might ultimately prove separate generically but at present I cannot determine a clear diagnosis of such a genus and these species fit the current concept of *Clematocrinus*. Moreover, phylogeny within the family as in Ubaghs (1978b) is unclear and unnecessary introduction of further names seems unhelpful.

**Clematocrinus argylensis** sp. nov.
(Fig. 41)

ETYMOLOGY. From just east of the Argyle Railway Station near Heathcote.

MATERIAL. HOLOTYPE: NMVP109188. PARATYPES: 109189, 109193, 109201 from NMVPL2259.

DIAGNOSIS. Cup bowl-shaped. Posterior interray with vertical anal tube. Radials about half cup length, with extremely narrow radial facets less than half plate width. Arms 10, uniserial, of subrectangular (in lateral view) to cuneate brachials. Stem noncirriferous, with crenulate intercolumnal sutures, with columnals becoming longer and epifacet not breaking up into tubercles distally.

DESCRIPTION. Crown elliptical, 25mm long. Cup bowl-shaped, about 5mm long, radially symmetrical except for posterior interray, without basal concavity. Cup plates smooth, thin. Basals 3, fully exposed laterally, with circular crenulate stem attachment occupying central 1/3 of diameter. Radials 5, largest plates in cup, about 1/2 cup length, hexagonal; radial facet horizontal, about 1/3 radial width. Arms 10, free distal to primaxil, uniserial; 1st primibrach subquadrate, with convex raised central part and depressed lateral flanges; 2nd primibrach pentagonal, axillary, fixed in cup, with depressed lateral flanges; brachials variable in proportions but usually longer than wide, subpentagonal proximally, rapidly becoming cuneate distally; pinnules one per brachial, alternating along each arm, long, becoming more slender distally, of long pinnulars (4-8 per pinnule). Proximal interprimibrach large, hexagonal, resting on shoulders of adjacent radials, only interbrachial in cup; CD interray with row of 3 anal plates resting on shoulders of contiguous radials, with anals forming vertically

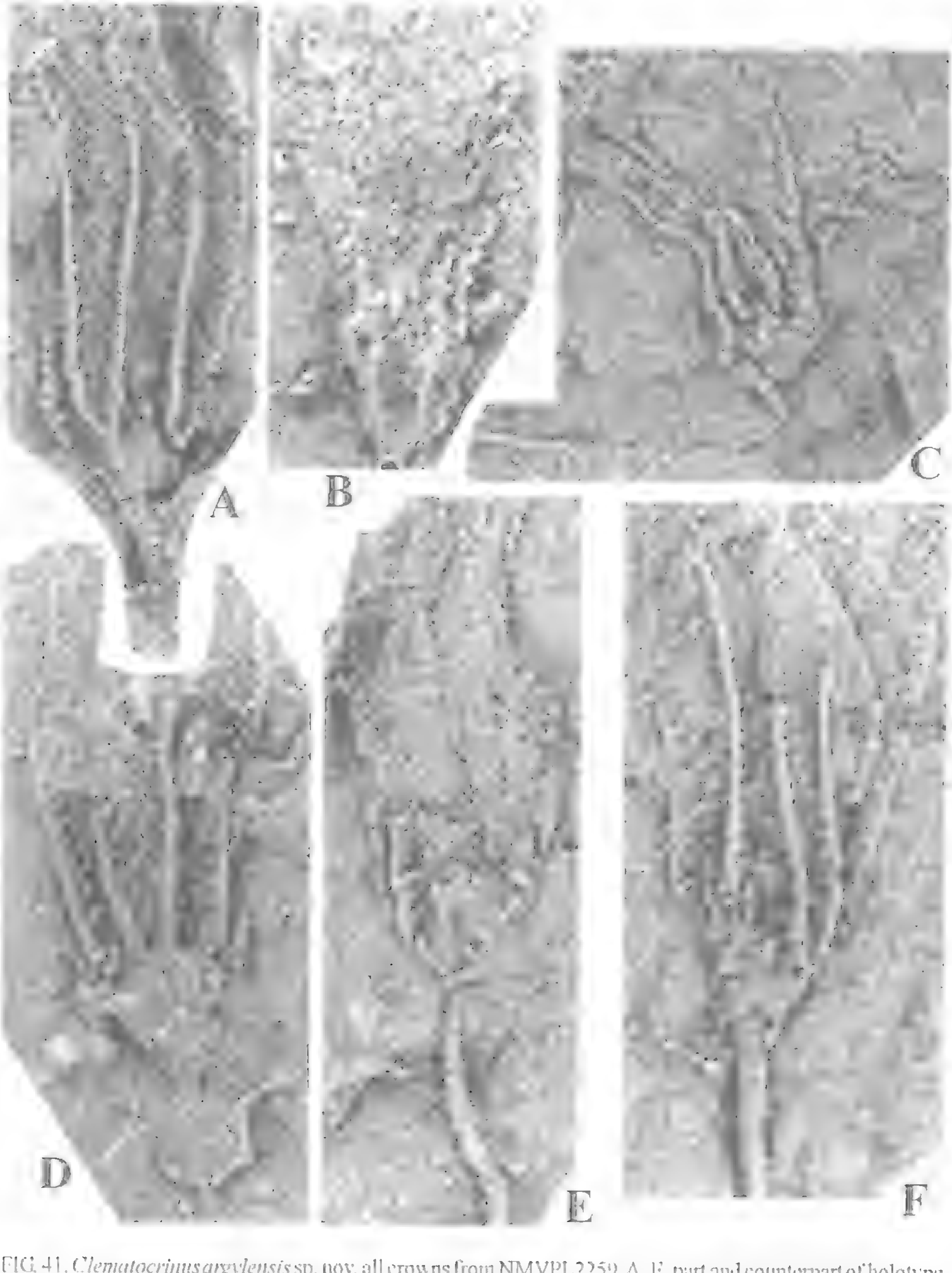


FIG. 41. *Clematocrinus argylensis* sp. nov. all crowns from NMVPL2259. A, E, part and counterpart of holotype NMVP109188, ×4.5 and ×4, respectively. B, NMVP109201, ×6. C, NMVP109193, ×6. D,F, part and counterpart of NMVP109189, ×4.

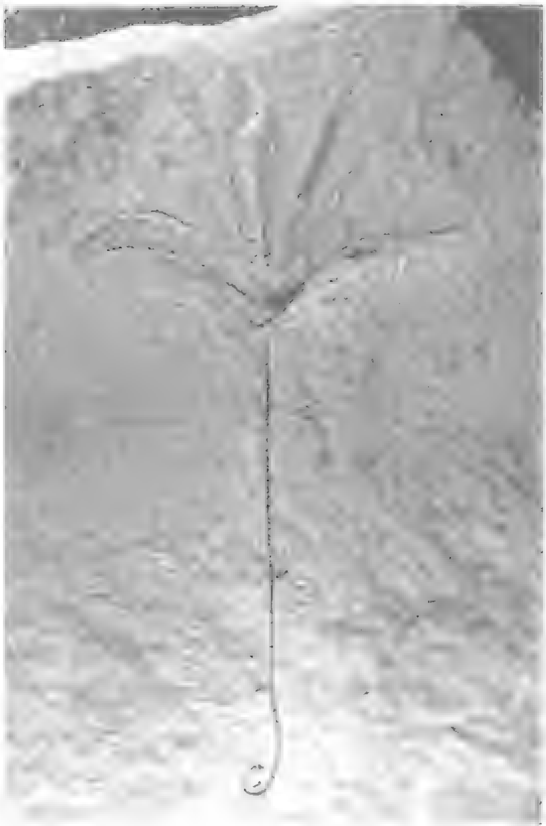


FIG. 42. *Helicocrinus plumosus* Chapman, 1903, holotype, NMVP384, from a quarry in West Brunswick Melbourne, ×1.7.

elongate anal tube; primanal central, pentagonal, smaller than proximal interbrachial of normal interrays, flanked by smaller anal tube plates in contact with primibrachs. Stem circular in section, heteromorphic; proximally with alternating nodals and internodals of similar length but with epifacets or annular flange at midlength of latus being wider on the nodals; distally with uniform columnals, each with the epifacet at midlength of latus.

REMARKS. This species is close to *C. perforatus* but has narrower radial facets and arms, different stem and longer unfused basal circlet.

**Helicocrinus** Chapman, 1903

TYPE SPECIES. *Helicocrinus plumosus* Chapman, 1903 from the Ludlow of Melbourne, by monotypy.

REMARKS. Ubaghs (1978b) suggested that this genus was 'Possibly a hapalocrinid' although placing it in the group of uncertain taxonomic placement. Chapman (1903) had noted the same alliance originally and no contrary opinion has been offered. The present state of the holotype and only specimen makes definite assignment impossible but the discussion of that specimen below gives confidence to a family assignment in the Hapalocrinidae. I recommend that since critical features of the holotype are not now retrievable the generic name should be confined to the holotype and isolated on that specimen. Although it may seem likely that *Clematocrinus perforatus* sp. nov. should belong to the same genus there is no proof of this and it is better not to compound the problem by extending use of such a poorly defined name. Nevertheless, occurrence of 5, and probably more, species of Hapalocrinidae in Victoria demonstrates that the family was successful in this region during the Late Silurian. *Helicocrinus* may be separated from known Hapalocrinidae by the distally coiled stem with pentagonal section.

**Helicocrinus plumosus** Chapman, 1903
(Fig. 42)

MATERIAL. HOLOTYPE: NMVP384 from a quarry at West Brunswick, between Albert and Victoria Streets. The matrix into which this individual was moulded is soft and friable; I have not made a latex cast because I consider it likely damage would be caused to the type.

REMARKS. Chapman (1903, pl. 18, figs 1-5) provided drawings of various parts of the holotype that are not clear from his photograph or from the holotype today. The holotype shows signs of having been damaged through efforts at preparation somewhere in the intervening 80 years since discovery but it may also be significant that in his description Chapman did not allude to any features of the cup plating. Even his drawing of the cup is incomplete just distal to the radials. Since the primibrachs are critical for species and genus recognition it is impossible to accommodate this specimen within current taxonomic concepts.

**Hapalocrinidae** indet.
(Fig. 43)

MATERIAL. NMVP107091 from the South Yarra Brick-works dump originally from excavations in the Ludlovian Melbourne Formation at the eastern end of Melbourne City area; collected by Leo Stach of Melbourne High School.

REMARKS. This 28mm long crown is preserved in a medium to coarse micaceous sandstone so that interplate sutures are not clear anywhere on the specimen. However, the cup is high conical

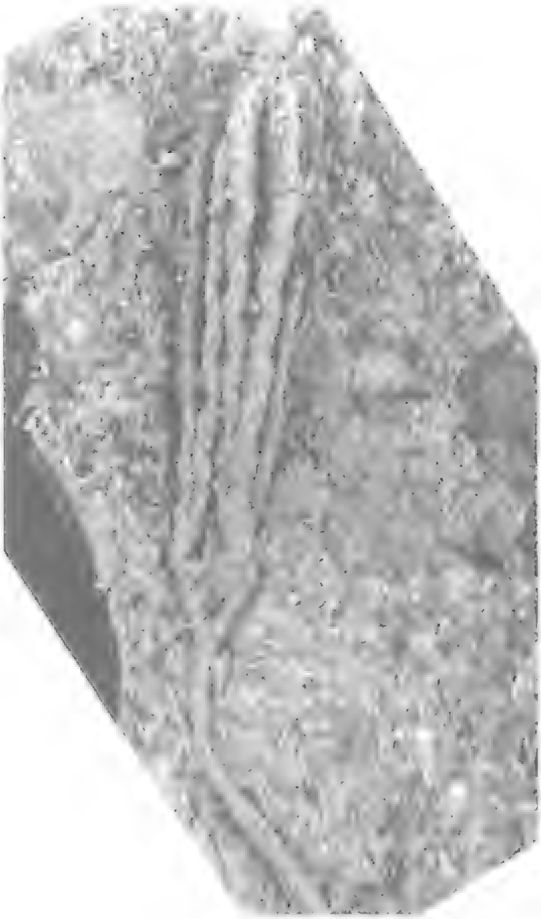


FIG. 43. Hapalocrinidae indet., posterior view of crown NMVP107091 from the South Yarra Brickworks Dump originally from excavations at the eastern end of Melbourne CBD, ×3.

and the general impression of radials and basals is discernible with a vertical (anal) tube beginning above the radials and extending up between the arms. There are 10 pinnulate arms; details of the stem are unclear except that there appear to be circlets of tubercles and some perforations distally. This meagre combination of features allows the specimen to be interpreted as a posterior view of a hapalocrinitid but generic determination appears impossible.

Subclass DISPARIDA Moore & Laudon, 1943
Superfamily CALCEOCRINOIDEA Meek & Worthen, 1869
Family CALCEOCRINIDAE Meek & Worthen, 1869

**Darraghcrinus** gen. nov.

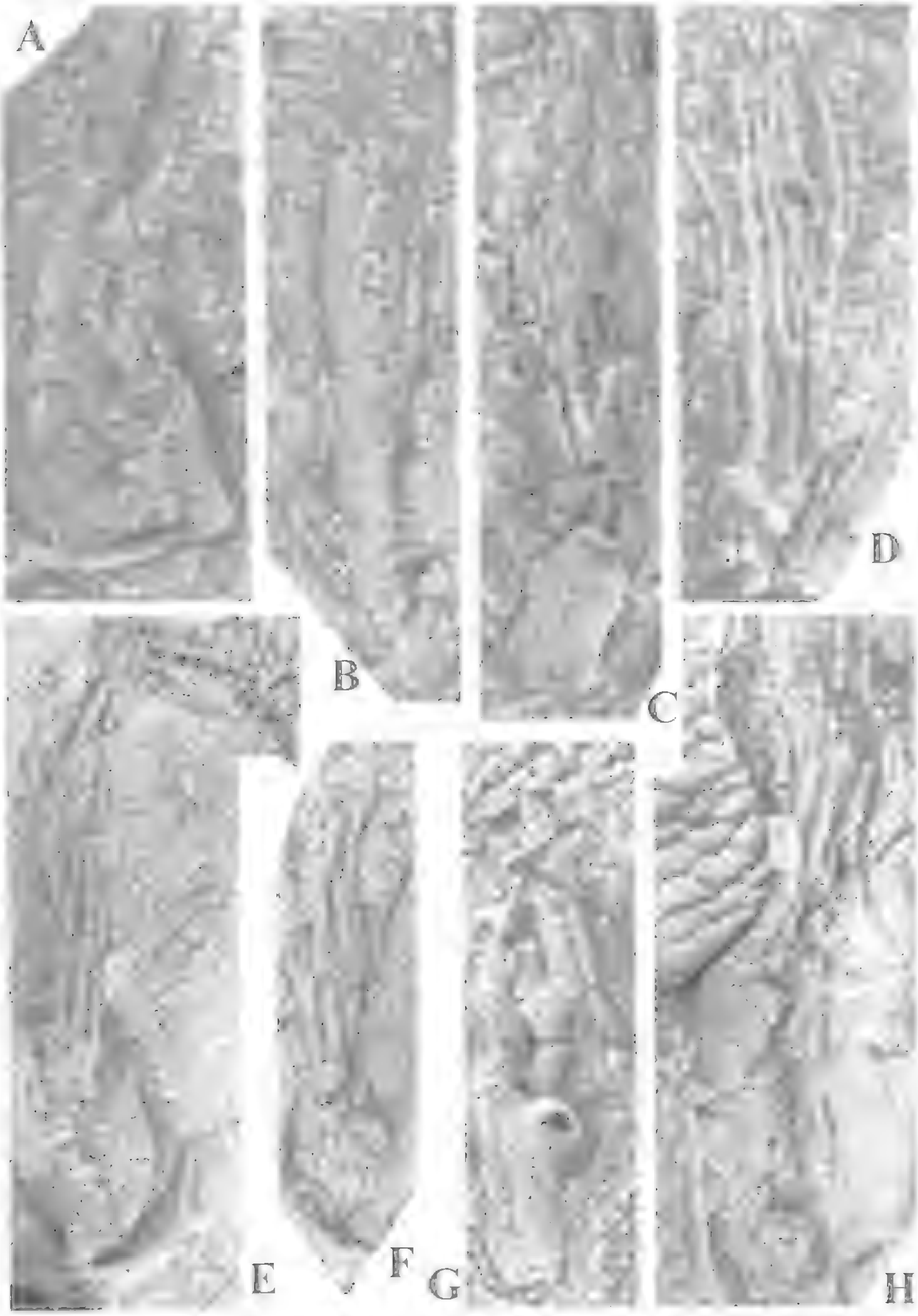
TYPE SPECIES. *Darraghcrinus tomi* sp. nov.

ETYMOLOGY. For Tom Darragh of the Museum of Victoria.

DIAGNOSIS. Cup elongate, waisted near mid-length, bilaterally symmetrical; E radial divided into small triangular supero- and inferoradials separated by long suture separating large lateral A and D radials; basal circlet semi-elliptical, of 3 plates, with two tiny plates and large triangular posterior plate, with stem attachment in contact with all 3 plates. E ray arm with or without a single division at primibrach 13; lateral arms with axillary 2nd primibrach, with subsequent isotomous divisions on both resulting branches (ramules and main axil series not evident).

DISCUSSION. Moore (1962) reviewed the phylogeny of the Calceocrinidae indicating 2 Ordovician to Devonian lineages distinguished by the degree of symmetry of the crown and his phylogeny has largely been accepted by subsequent workers (Arendt, 1965; Prokop, 1970). Since this Australian species has perfect bilateral symmetry it must belong to Moore's group arising from *Calceocrinus*. However, Moore (1962) also indicated the trend in this group towards development of main axils with ramules. In the Australian species main axils are not developed; A and D radials each support a lateral arm that divides isotomously twice, indicating that neither of the 2 branches from the first division can be considered a ramule. These features are sufficient to isolate the Australian species at generic level and to throw into doubt its possible affinities. The cup of *D. tomi* is very similar to that of *Eohalysiocrinus* Prokop, 1970 from the Devonian of Bohemia. Prokop (1970) did not figure specimens with arms but nevertheless provided a reconstruction with a single lateral arm on the A radial (and presumably another, not seen, on the D radial) that branches on the 2nd primibrach and then each branches again on the 3rd secundibrach; he identified primaxil and

FIG. 44. *Darraghcrinus tomi* gen. et sp. nov., all crowns from NMVPL252. A, lateral view of NMVP108653, ×4. B,D, part and counterpart of NMVP110637, ×3. C, E ray view of NMVP110635, ×4. E,F, part and counterpart of NMVP108654, ×4. G, D ray view of NMVP110640, ×7.5. H, oblique E ray view of NMVP108625, ×5.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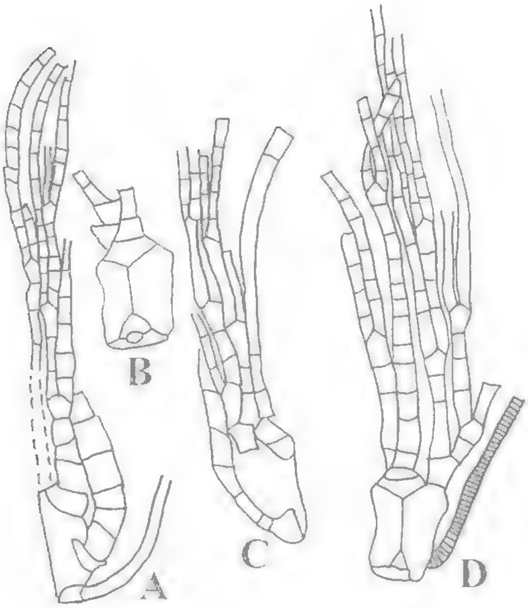



FIG. 45. *Darraghcrinus tomi* gen. et sp. nov., sketches of plate arrangement of A, NMVP108654a (Fig. 44E); B, NMVP110635 (Fig. 44C); C, NMVP108654b (Fig. 44F); D, NMVP110637a (Fig. 44D).

secundaxil arms and a ramule. While this branching pattern has some similarity with *D. tomi* there are distinct differences: branches after divisions in *D. tomi* are of equal diameter, the primibrach is much longer and narrower in *D. tomi* and the E ray arm is of similar diameter to the lateral arms. Brett (1981) indicated that Prokop's reconstruction of the arms is 'completely hypothetical' and showed an advanced arm branching pattern with main axil structure in *Eohalysiocrinus typus* from the Silurian of North America. Nevertheless, the cup of *E. typus* is very similar to that of *D. tomi* in observable features, particularly on the anterior side. Notably, however, Brett's species has a different arm branching pattern, anal tube completely enclosed by the arms and E ray brachials much larger than those of the lateral arms.

In the context of Moore's phylogeny *D. tomi* cannot be easily linked to any of the known Devonian members of the family. Its arm branching pattern seems akin to the most primitive members of the family or even the ancestral group, yet its cup resembles some of the most advanced Devonian taxa. I assign this genus to the Calceocrinidae with confidence but cannot suggest a reasonable ancestral lineage from among known forms.

**Darraghcrinus tomi** sp. nov.
(Figs 44-46)

MATERIAL. HOLOTYPE: NMVP149347. PARATYPES: NMVP108625, 108651, 108653, 108654, 108656, 110634, 110635, 110637-110640, 149363 from NMVPL252.

DIAGNOSIS. As for genus.

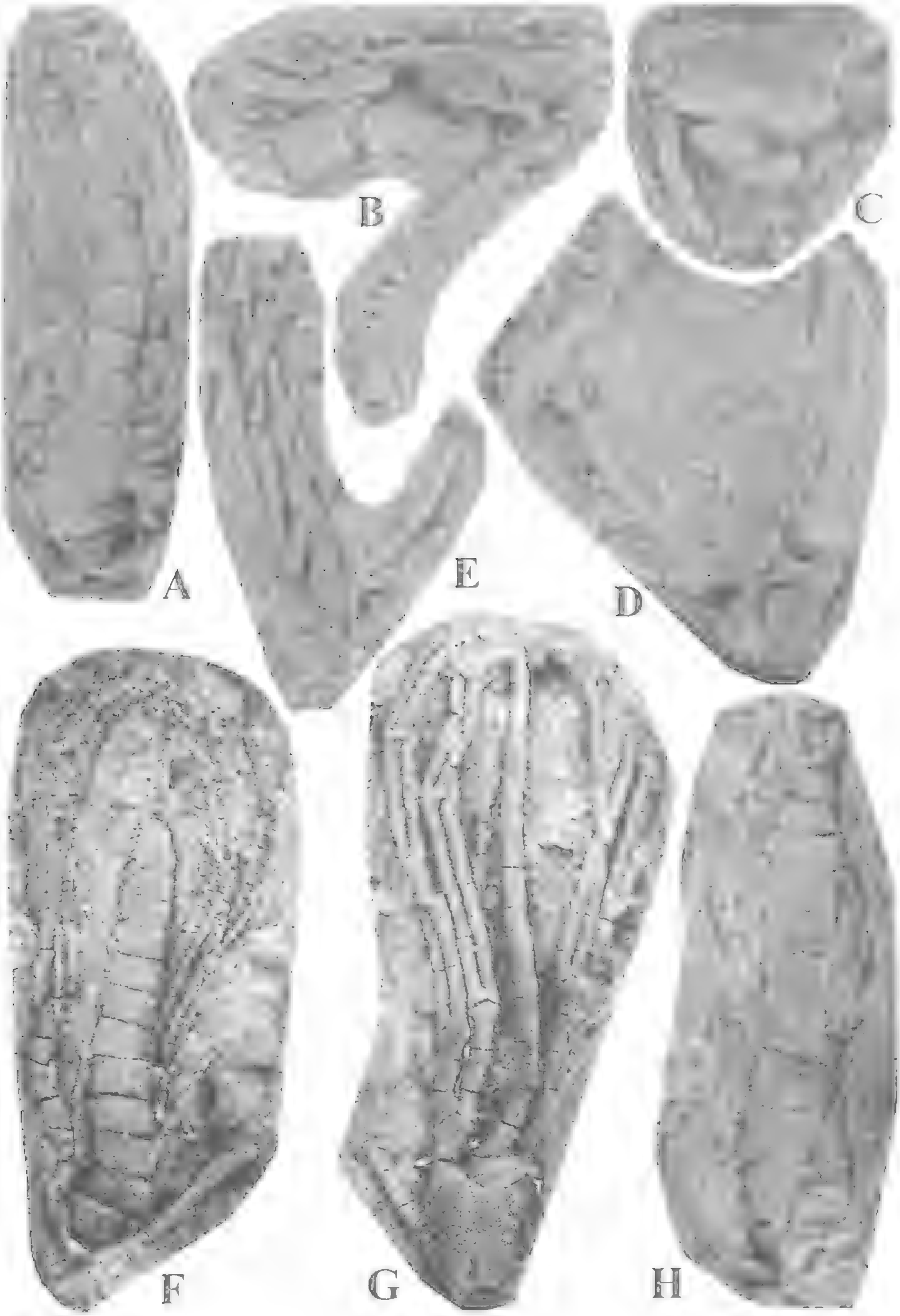
DESCRIPTION. Crown up to 36mm long. Calyx subrectangular in E ray view (c. 20% longer than wide), slightly waisted near midheight; E ray side of cup flat to weakly concave, opposite (posterior) side convex. Plates with finely granulose surface, with stereom structure of plates clear in most specimens.

Basal circlet not clear in any one specimen but inferred from parts of several; semi-elliptical, 3 plates, stem attachment straddling suture between two larger ones, third triangular much wider than long and occupying most of circlet.

E ray (median) inferoradial and superoradial widely separated by A and D radials; separation distance more than 1/2 cup height. Small, triangular E-ray inferoradial occupying just over 1/3 basal cup width; lower margin with a rectangular ligament fossa, bounded on each side by dentate projections of inferoradial. E-ray superoradial also triangular, 3 times as broad as long, extending above the A and D radials; radial facet broad, nearly circular.

Lateral (A and D) radials very large, enclosing cup laterally, extending onto posterior side; subanal plate (fused B and C radials) low, wide, only slightly recessed for anal X; anal X large, identical to more distal anal plates, bounded laterally by A and D radials and subanal, with rounded lower corners, occupying most of posterior side of cup. Anal tube projecting posteriorly from cup, curving anteriorly upwards to be enveloped by the lateral arms above midheight, of large laterally convex rectangular plates on posterior side, tapering slightly in upper half, rounded upper end, with anterior side of lower subrectangular plates.

FIG. 46. *Darraghcrinus tomi* gen. et sp. nov., all crowns from NMVPL252. A, lateral view of NMVP110639, ×4.7. B, lateral view of damaged cup with stem NMVP108651, ×4.7. C, small theca with stem NMVP108653b, ×5.7. D,E, part and counterpart of crown attached to large *Sphenothallus* NMVP110638a and B, ×3.3. F,G, lateral views of part and counterpart of holotype NMVP149347, ×4.7. H, lateral view of NMVP110634, ×5.7.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Arms 3; E-ray arm branching isotomously once high above cup, with 12 primibrachs, 12th axillary; 1st primibrach subtrapezoidal, tapering distally; rest of arm more or less uniform in section; interplate sutures poorly defined. A and D radials with 2 primibrachs, 2nd axillary; on more anterior branch 3rd or 4th secundibrach axillary, with 4th or 5th tertibrach axillary above that on posterior branch and with anterior branch undivided; on posterior branch of original division 2nd secundibrach axillary on posterior branch and 3rd or 4th tertibrach on anterior division axillary, then 4th quartibrach axillary on posterior branch (Fig. 44D); each arm tapering near base but mostly of uniform diameter.

Stem circular in section, of short laterally convex columnals, with columnals becoming slightly longer and less convex laterally away from cup; attachment simple cementation, observed in two cases to be cemented to large specimen of *Sphenothallus*.

Superfamily PISOCRINOIDEA Angelin, 1878
Family PISOCRINIDAE Angelin, 1878

**Trichocrinus** Müller, 1856

TYPE SPECIES. *Trichocrinus altus* Müller, 1856 from the Middle Devonian of Germany; by monotypy.

REMARKS. Moore et al. (1978) considered *Trichocrinus* a junior synonym of *Triacrinus* Munster, 1939 from the Late Silurian and Devonian of Europe. Rozhnov (1981) separated them and characterised *Trichocrinus* as having a longer, regularly conical, cup of smaller diameter as opposed to convex-conical shape with lobate profile in distal view, a shallow or no basal concavity for stem facet and a 'different form of distal growth'.

Rozhnov (1981, fig. 9) also provided a phylogeny showing *Triacrinus* and *Trichocrinus* evolving from different subgenera of *Pisocrinus*. I accept Rozhnov's generic concepts and phylogeny and assign this Victorian species to *Trichocrinus* with its tall conical cup lacking basal concavity. *T. morleyi* from the Ludlow is among the oldest known species of the genus and greatly extends its geographical range. Its occurrence in Australia may be significant in view of the Upper Devonian, Western Australian *Jaekelicrinus* (Jell & Jell, 1999) which genus belongs to the same lineage as *Trichocrinus*.

**Trichocrinus morleyi** sp. nov.
(Figs 47, 48)

ETYMOLOGY. For David Morley who drew my attention to the occurrence of crinoids at the type locality.

MATERIAL. HOLOTYPE: NMVP100111. PARATYPES: NMVP100103, 100105, 100110, 100113-100115, 107108-107110, 109827 all from NMVPL1923. NMVP148608, 148611, 148612 from Moonee Ponds Creek; NMVP111845, 148624 from NMVPL299; NMVP391 from NMVPL1615.

DIAGNOSIS Cup with 3 basals, long, with rounded distal margin to inferradial. First primibrach short, tapering upwards. Arms 5, atomous, of long brachials, 5-10 times length of cup. Stem long, heteromorphic, of alternating columnals proximally becoming strongly beaded distally.

DESCRIPTION Crown small, with very long arms up to 10 times as long as cup. Cup approximately twice as long as wide, smooth. Basals 3, forming circlet only marginally wider than long. Radials smooth, with A and D radials more than twice as long as wide, with E radial small triangular and taking part of distal corner from both A and D radials (more from D than A); B superradial and C radial approximately same size as E radial but apparently with concave proximal margin; B inferradial large, with rounded distal margin, rotated to right (theca oriented with stem down) i.e. anticlockwise relative to superradial; all radials with vertical grooves on both plates at and normal to the radial to 1st primibrach suture. Anal X distal to cup, between the C and D primibrachs. Arms 5, atomous, 5-10 times as long as cup, nonpinnulate, laterally compressed, with deep adoral groove covered by 2 series of interlocking cover plates; 1st brachial subtriangular, with broad base on radial facet, lower than more distal brachials, twice as wide proximally as distally; other brachials more than twice as long as wide, of approximately uniform length through arm, with 8 pairs of adoral groove cover plates in contact with each brachial. Stem long but full extent not known, circular in section; columnals uniform in length proximally

FIG. 47. *Trichocrinus morleyi* sp. nov. all crowns in lateral view except for one cup (C and E) from NMVP1923. A, NMVP100103, ×3.5. B,G, part and counterpart of holotype NMVP100111, ×4.5. C,E, part and counterpart of NMVP100110, ×4.5 and ×7. D,F, NMVP100113 (to right in D) and part and counterpart of NMVP100114, ×3 and ×4.5, respectively. H, NMVP100115, ×3. I, NMVP107110, ×4.5. J, NMVP107108, ×4. K, NMVP107109, ×5.


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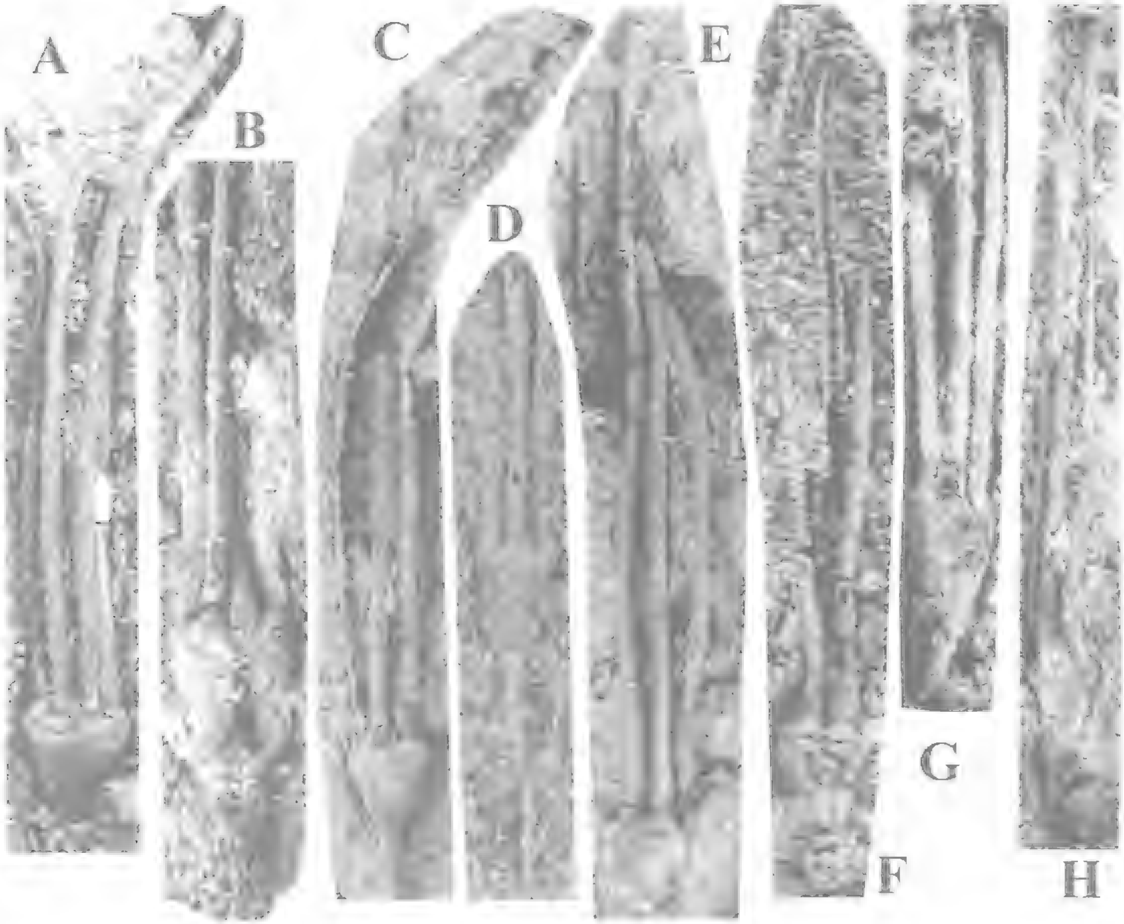
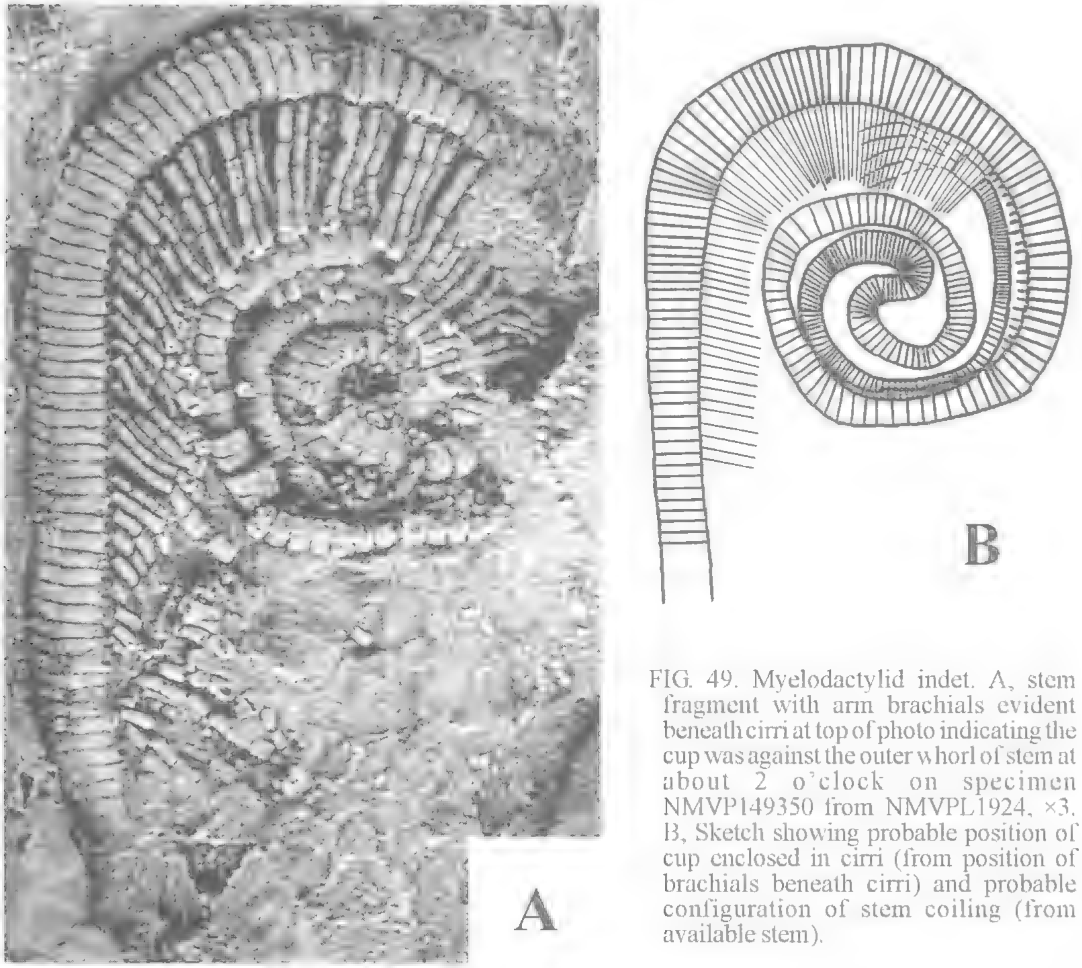



FIG. 48. *Trichocrinus morleyi* sp. nov., all crowns in lateral view. A,B, part and counterpart of NMVP148608 from Moonee Ponds Creek, ×3. C,E, part and counterpart of NMVP148624 from NMVPL299, ×3. D, NMVP111845, ×4. F, NMVP391 from NMVPL1615 (with type of *Nassoviocrinus longibrachiatus*), ×3. G, NMVP148612 from Moonee Ponds Creek, ×4. H, NMVP148611 from Moonee Ponds Creek, ×3.

but alternating long and short distally, diameter decreasing uniformly and rapidly through 10 most proximal, then uniform for variable distance of between 30-200 columnals, then alternating large and small to give a beaded appearance to most of stem.

REMARKS. This species is closely related to *T. elongatus* Follmann, 1887 and *T. altus* Muller from the Lower Devonian Hunsrück Shale of Germany but differs in its shorter arms with longer more uniform brachials, its longer basals, rounder distal margin to the B inferradial, and more noticeably beaded distal stem. Several species of *Pisocrinus* grouped by Rhozhnov (1981) as *P. (Pocillocrinus)* and exemplified by *P. (P.) pocillum* Angelin, 1878 from the Late Silurian of Gotland have similarly shaped cups as remarked by Bather (1893:23), are part of a lineage among long species from 5 basals to 3 and prompt the question of whether the number of basal plates is a watertight generic distinction. Since the same reduction occurs in other groups (e.g. the Synbathocrinidae — *Phimocrinus* to *Synbathocrinus*) it is clear that numerous lineages involved reduction in numbers of basals. Since Rozhnov (1981) identified the separate lineages leading from *Pisocrinus* to forms with 3 basals the question now arises whether he has identified all the lineages in the family or did the 5 to 3 basals transition occur more than twice in the Pisocrinidae? Could there have been a separate lineage in Australia evolving in parallel



A B

FIG. 49. Myelodactylid indet. A, stem fragment with arm brachials evident beneath cirri at top of photo indicating the cup was against the outer whorl of stem at about 2 o'clock on specimen NMVP149350 from NMVPL1924, ×3. B, Sketch showing probable position of cup enclosed in cirri (from position of brachials beneath cirri) and probable configuration of stem coiling (from available stem).

to the European lineages outlined by Rozhnov (1981) or, as seems most likely at present, did the Australian pisocrinids migrate iteratively from Eurasia during the Ludlow, and the Upper Devonian?

Several specimens (Fig. 48) assigned to this species from other than the type locality are preserved in medium to coarse sandstone; in these, details of plate boundaries are not always clear so assignment is made on cup shape, on length of arms and on the anal X above the cup.

Superfamily MYELODACTYLOIDEA S.A. Miller, 1883
Family MYELODACTYLIDAE Miller, 1883

**Myelodactylid** indet.
(Fig. 49)

MATERIAL. NMVP149350 from NMVPL1924.

DESCRIPTION. Proximal or evolute part of stem composed of many short columnals compressed in the plane of coiling and with a shallow narrow groove along the curved visible edge of the stem. Midsection or 2 inner involute whorls with longest columnals of whole stem, also compressed in the plane of coiling, with stout cirri on each columnal. Distal section or outer involute whorl apparently less compressed, stongly convex on outer side with groove on side (presumably one on other side as well) of central peak, with long cirri on each columnal.

REMARKS. Details of members of this family are available from a number of taxa well-preserved as original carbonate (Bather, 1893; Springer, 1926) with crowns well displayed. In the available Victorian external mould the crown is indicated by a number of arms beneath the cirri of the outer whorl; taking this indication with the direction of the proximal stem the crown is

inferred to have been adjacent to the outer whorl about 3/4 of the way around. Without the crown I do not attempt generic assignment as advocated by Eckert & Brett (1985) but the strongly coiled stem with differentiated proximal part, strong development of cirri, and indicated position of the crown all confirm the family assignment. The specimen is included here as an indication of the family's occurrence in Australia and warning to future collectors to seek out this interesting but relatively rare group of crinoids.

Superfamily BELEMNOCRINOIDEA
S.A. Miller, 1883

This superfamily as constituted by Moore et al. (1978) is a heterogeneous grouping of widely differing, mostly very small, crinoids whose affinities are often unclear. Rozhnov (1981) reassigned *Quiniocrinus* Schmidt, 1941 from the Perissocrinidae to the Pisocrinidae and Prokop & Petr (1997) suggested that *Storthingocrinus* is a camerate related to the Platycrinitidae; reassignment of other taxa grouped in this superfamily in 1978 seems likely.

Family PYGMAEOCRINIDAE Strimple, 1963

This family is monotypic and has been reviewed in detail by Prokop & Petr (1997). The new genus described here initially looks quite different from the Czech type species but comparison with Prokop & Petr's (1997) emended diagnosis reveals that the only difference between Czech and Australian taxa is in the number of brachials in each arm. *Pygmaeocrinus* Bouska, 1947 must be considered a derived form in the structure of its arms which consist of just 2 brachials, a small 1st and large widened 2nd that fully enclose the cup distally and *Kroppocrinus* can be considered a reasonable intermediate from a synbathocrinid like *Phimacrinus hanschi* sp. nov. which has 5 basals and an anal plate almost expelled from the cup. *Kroppocrinus* has the 5 basals but fewer brachials per arm and no anal plate. Thus I suggest that as a probable ancestor this new genus should be placed in the Pygmaeocrinidae.

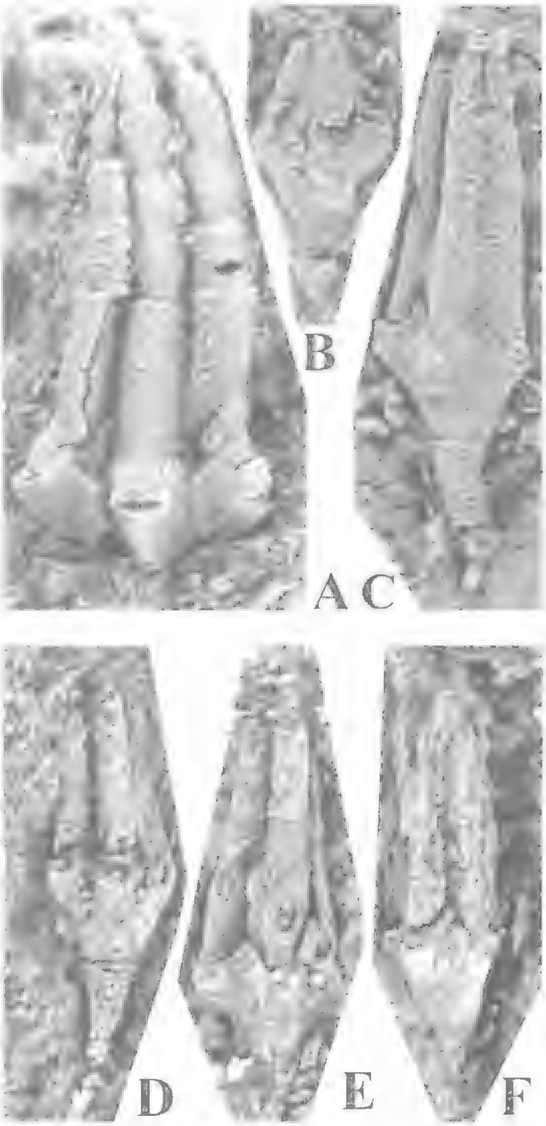



FIG. 50. *Kroppocrinus heathcotensis* gen. et sp. nov., all crowns in lateral view from locality 36 of Talent (1965, fig. 1) at Heathcote except A from NMVPL229. A, NMVP107106, ×6. B, NMVP-107093, ×7. C,E, part and counterpart of holotype NMVP107094, ×10. D,F, NMVP107092, ×9.

**Kroppocrinus** gen. nov.

TYPE SPECIES. *Kroppocrinus heathcotensis* sp. nov.

ETYMOLOGY. An anagram from Prokop plus the usual ending *-crinus*; for Rudi Prokop, Prague who has contributed to knowledge of Bohemian echinoderms.

DIAGNOSIS. Crown more than 3 times as long as cup. Arms in close lateral contact forming a tall conical enclosed space, with 5 or 6 brachials; 1st small, subquadrate, set into outer notch of radial facet; 2nd very large, up to 4 times as long as wide, with widest point above upper limit of radial's interradial peak, with series of horizontal ridges laterally on inner side; more distal brachials less than half as long as 2nd, of different lengths in different arms. Stem either attached to

rimmed facet in centre of flat cup base or same diameter as cup base but tapering rapidly distally; in latter case columnals low, uniform proximally becoming longer and heteromophic distally.

REMARKS. These 2 species are quite different in the size of the stem relative to the cup proximally and recessed basals laterally on cup on one but not other. However, cup shape and details of the arms are so similar that they are confidently assigned to the same genus herein. *K. mathiesonensis* has cup features linking it to *Pygmaeocrinus notabilis* Prokop & Petr, 1997 namely, the flat cup base with small rimmed stem attachment facet, depressed triangular distal extremities of the basals in view laterally and shape and projection of radials; however, it is the only specimen available and it has one branching 2nd brachial making it probably an aberrant specimen and therefore, unsuitable for type genus status. *K. heathcotensis* has less distinctive link to *Pygmaeocrinus* having a similar cup shape to *P. fabulosus* Prokop & Petr, 1997 but without unique characters. Nevertheless, it is a far more suitable species to stand as type since it is represented by several specimens and has the atomous arms considered typical of the genus.

**Kroppocrinus heathcotensis** sp. nov.
(Fig. 50)

ETYMOLOGY. From near Heathcote, central Victoria.

MATERIAL. HOLOTYPE: NMVP107094. PARATYPES: NMVP107092, 107093 all from Locality 36 of Thomas (Talent, 1965, fig. 1); paratype NMVP148560 from locality 41 of Thomas (Talent, 1965, fig. 1); paratype NMVP107106 from NMVPL229.

DIAGNOSIS. Cup evenly flaring in proximal part, same diameter as stem at their junction, with concave lateral cup margin due to extended radial facets.

DESCRIPTION. Crown bipyramidal, pentalobate in section through radials or more distal, up to 12mm long. Cup 2-4mm long and wide, flaring uniformly distally in basal part but increasing in distal part of radials producing concave outer profile. Basals 5, circlet occupying about 1/4 cup length, not well defined, with low obtuse peaks at interradial sutures. Radials 5, subrectangular, longer than wide, expanding strongly laterally to facet, with sharply pointed interray peaks; radial facet deep narrow notch, slightly declined outwards. Arms 5, atomous, in lateral contact throughout forming tightly closed space within, with horizontal ridges laterally on

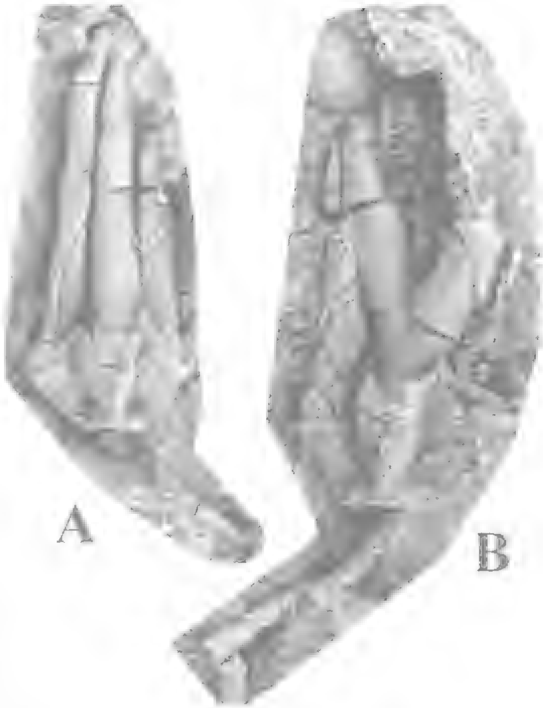



FIG. 51. *Kroppocrinus mathiesonensis* gen. et sp. nov., part and counterpart of holotype crown NMVP-109752 from NMVPL1924, ×4 and ×6 respectively.

inner surface of brachials interlocking with adjacent brachials; brachials 5 per arm; 1st short; 2nd very long; distal ones of variable lengths within and between arms so adjacent arms may have distal interbracial articulations at different levels. Stem same diameter as base of cup at attachment; proximal part tapering strongly, of very short columnals of uniform length; distally heteromorphic, slightly wider and longer nodals alternating with very short internodals.

REMARKS. This species is distinguished from *K. mathiesonensis* by nature of cup base and nature of stem. The available specimens have some hardened limonitic infills in the moulds which result in the slightly incomplete latexes illustrated but taken in combination available specimens provide a clear species concept. Although not figured, features of distal parts of the stem are available on NMVP148560.

**Kroppocrinus mathiesonensis** sp. nov.
(Fig. 51)

ETYMOLOGY. From Mathieson's Creek, near Kinglake.

MATERIAL. HOLOTYPE: NMVP109752 from NMVPL1924.

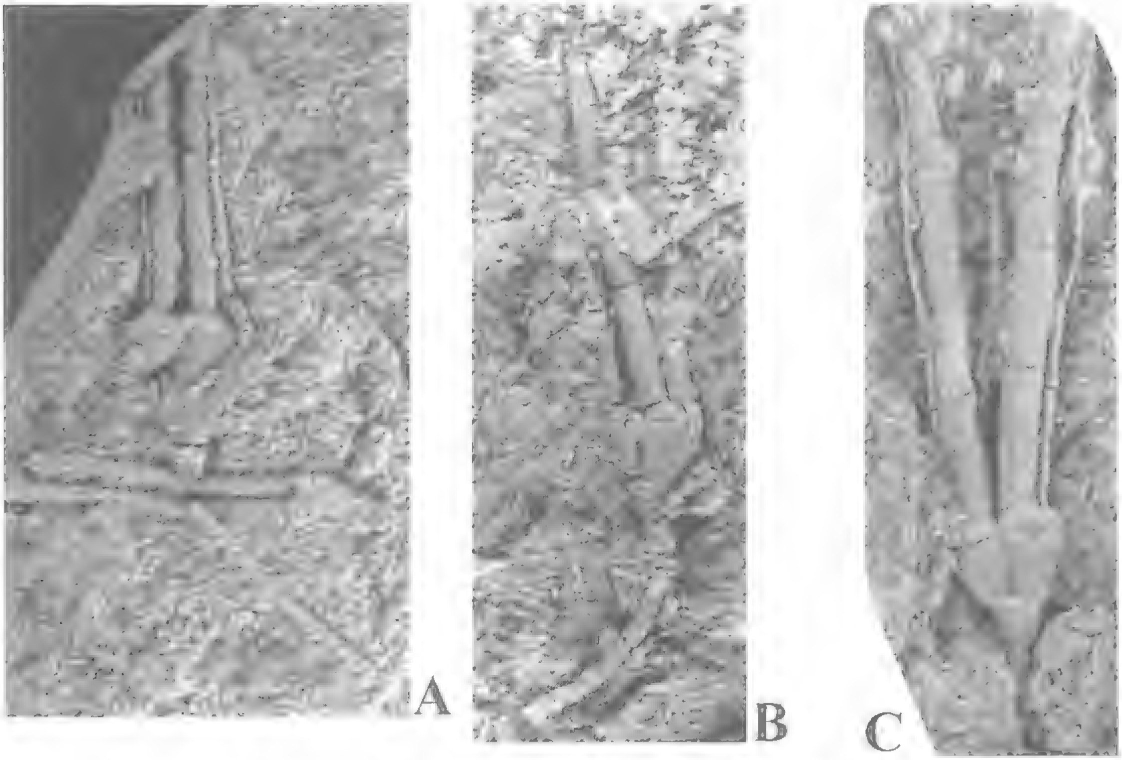


FIG. 52. *Phimocrinus americanus* Springer, 1923, all crowns in lateral view. A, NMVP109206 from NMVPL1615, ×5. B, NMVP100151 from NMVPL229, ×3. C, NMVP109205 from NMVPL229, ×4.

DIAGNOSIS. Cup with flat base, much greater in basal diameter than proximal stem, with straight distally flaring outer wall. Basals as depressed interradial triangles in lateral view extending distally from cup base.

DESCRIPTION. Crown bipyramidal, pentastellate in section through radials or more distal, up to 7mm long. Cup 2mm long and wide, flaring uniformly distally giving straight outer profile. Basals 5, occupying most of flat cup base and depressed triangles interradially in side walls of cup. Radials 5, subrectangular but with prominent, strongly constricted base between basals, longer than wide, expanding strongly in midline to facet, with sharply pointed interray peaks; radial facet deep narrow notch, declined outwards. Arms 5, atomous, in lateral contact throughout, forming tightly closed space within, with horizontal ridges laterally on inner surface of brachials interlocking with adjacent brachials. Brachials 5 per arm, 1st short, 2nd very long, distal ones of variable lengths within and between arms so adjacent arms may have distal interbracial articulations at different levels. Stem of much smaller diameter than cup base, of uniform diameter except for very small expansion towards cup in most proximal part; columnals uniform, short, separated by crenulate sutures.

REMARKS. The most obvious comment on this specimen has to be on the bifurcate arm (Fig. 51B). In view of the related type species *K. heathcotensis* having its arms tightly closed and the other 4 arms of this specimen appearing the same, this bifurcate arm is here considered aberrant, probably the result of damage and regrowth. How the animal lived without being able to seal the space within the arms is not clear because that seems to have been a functional requirement of this group of crinoids, judging from other available material. I have not, therefore, included this in features of the species even though I do not have available a specimen to prove that this is an aberrant specimen.

## Family SYNBATHOCRINIDAE S.A. Miller, 1883

### **Phimocrinus** Schultze, 1867

TYPE SPECIES. *Phimocrinus laevis* Schultze, 1867 from the Middle Devonian of Germany.

REMARKS. This genus is separated from *Synbathocrinus* principally on its 5 rather than 3 basal plates. However, some species of the latter genus have the basals fused so this feature is not clear cut. The 2 Australian species described here have much longer brachials than in any *Synbathocrinus* where the brachials are usually wider than long or subquadrate in lateral view; in the absence of arms for the European species this feature cannot be applied universally.

### **Phimocrinus americanus** Springer, 1923 (Fig. 52)

MATERIAL. HOLOTYPE: Springer, 1923, pl. 5, figs 17-19 from the Lower Devonian Linden Formation in Benton County, Tennesee; NMVP100151, 109205 from NMVPL229; NMVP109206 from NMVPL1615.

DIAGNOSIS. Cup evenly tapering, high conical, of smooth plates. Anal X notched into tops of adjoining C and D radials. Arms long, of elongate brachials.

DESCRIPTION. Cup small, up to 4mm long, high conical, smooth. Basals 5, short, with obtuse upper angle at interradial sutures. Radials long, forming most of cup, almost twice as long as wide, with horizontal distal suture; articular facet full width of radial; 1st primibrach short, tapering distally, sloping inwards so that bases of 2nd primibrachs remain in contact laterally but around a circle of smaller diameter than that of radials. Arms 5, atomous, straight, (probably laterally in contact throughout life), with broad shallow ambulacral furrow, cuneate in section; brachials of variable length, with some twice as long as others. Anal X small, triangular, nestled between C and D radials distally; anal tube extending up inside arms, full extent unknown. Stem circular in section, diameter small in relation to cup, with nodals just larger and more prominent than internodals; length unknown.

REMARKS. The single North American specimen lacks arms and stem but is matched in every available feature of the cup by the Australian specimens. There is no basis to separate these specimens from different parts of the world but future discovery of a complete specimen in North America could necessitate a new specific name for the Australian material.

FIG. 53. *Phimocrinus hanschi* sp. nov., holotype crown in posterior view, NMVP100648 from NMVPL300, ×2.5.

### **Phimocrinus hanschi** sp. nov. (Fig. 53)

ETYMOLOGY. For David Hansch of Melbourne who contributed specimens to this study.

MATERIAL. HOLOTYPE: NMVP100648 from NMVPL300.

DIAGNOSIS. Cup high conical, slender. Anal X strongly notched into radials. Arms long, that of C ray longer than others, of long brachials. Stem circular in section, slender, heteromorphic, with nodals longer than internodals.

DESCRIPTION. Cup small, up to 4mm long, high conical, very slender, smooth. Basals 5, short, about 1/4 of cup length. Radials long,

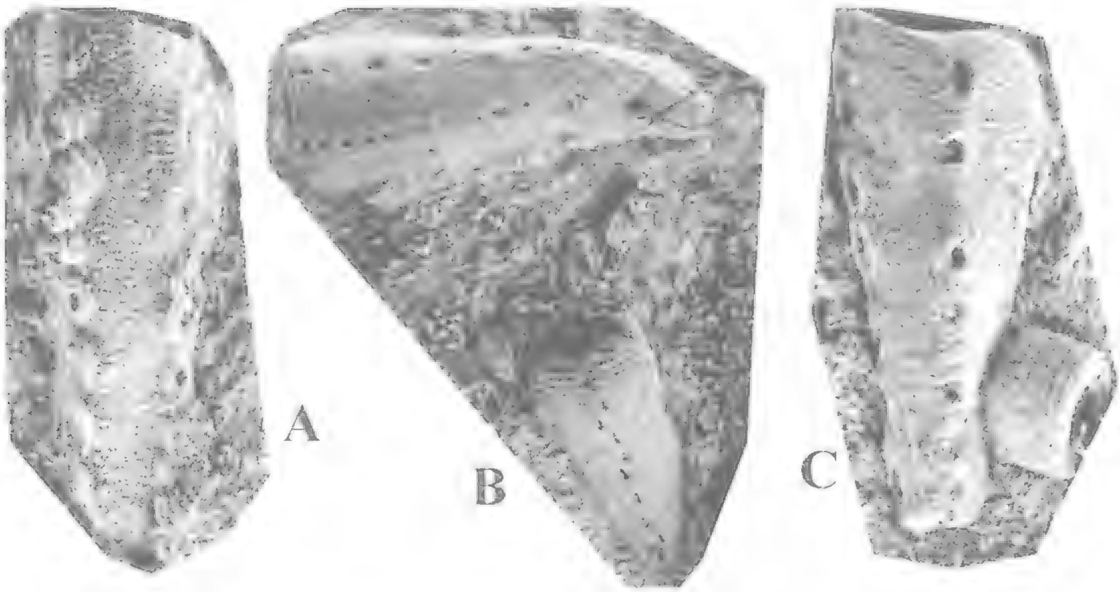



FIG. 54. *Crotalocrinites* sp., all distal stem elements of fused columnals with canals leading into cirri in 5 vertical columns from locality 54 of Talent (1965, fig. 1), ×1.2. A, NMVP149349. B, NMVP16789. C, NMVP149348.

forming most of cup, almost twice as long as wide, with straight distal suture; articular facet full width of radial, horizontal; 1st primibrach short, tapering distally and sloping inwards so that bases of 2nd primibrachs remain in contact laterally but around a circle of smaller diameter than that of radials. Arms 5, atomous, straight, (probably laterally in contact throughout life), with that in C ray about 1/3 again longer than other 4, with broad shallow ambulacral furrow, cuneate in section; brachials of variable length, with some twice as long as others. Anal X small, triangular, notched into distal corners of C and D radials; anal tube inside arms, full extent unknown. Stem circular in section, diameter small in relation to cup, with nodals just longer than internodals; length unknown.

REMARKS. In this species the basal part of the cup is very slender because the flaring of the cup occurs near the distal margins of the radials whereas in other species the cup flares near the base to be more bell-shaped. Arms are unknown for any Northern Hemisphere specimens so comparison is impossible but the elongate C ray arm distinguishes this species from *P. americanus* as interpreted from the Australian material described above.

Subclass CLADIDA Moore & Laudon, 1943
Order CYATHOCRINIDA Bather, 1899
Family CROTALOCRINITIDAE Bassler, 1938

**Crotalocrinites** Austin & Austin, 1843

TYPE SPECIES. *Cyathocrinites rugosus* Miller, 1821 from the Upper Silurian of England; by original designation.

**Crotalocrinites** sp. indet.
(Fig. 54)

MATERIAL. NMVP16789, 149348 and 149349 from locality 54 (Talent, 1965, fig. 1) in Unit 3 of the Mount Ida Formation, N of Heathcote.

REMARKS. These specimens are large (up to 20mm in diameter and 80mm long) disarticulated distal stem terminations. They are subpentagonal in section, have a line of perforations leading into stout cirri or rootlets along each angle and are ornamented with close spaced horizontal grooves arond the stem. This long section is almost certainly formed by fusion of numerous columnals with the horizontal grooves indicating the former columnal boundaries.

Distal stems of this type were described from the Silurian of the Urals by Militsina (1980, pl. 2, fig. 4; pl. 3, figs 3, 4) for *Crotalocrinites* and *Syndetocrinus* of the Crotalocrinitidae. The Russian material has a round rather than

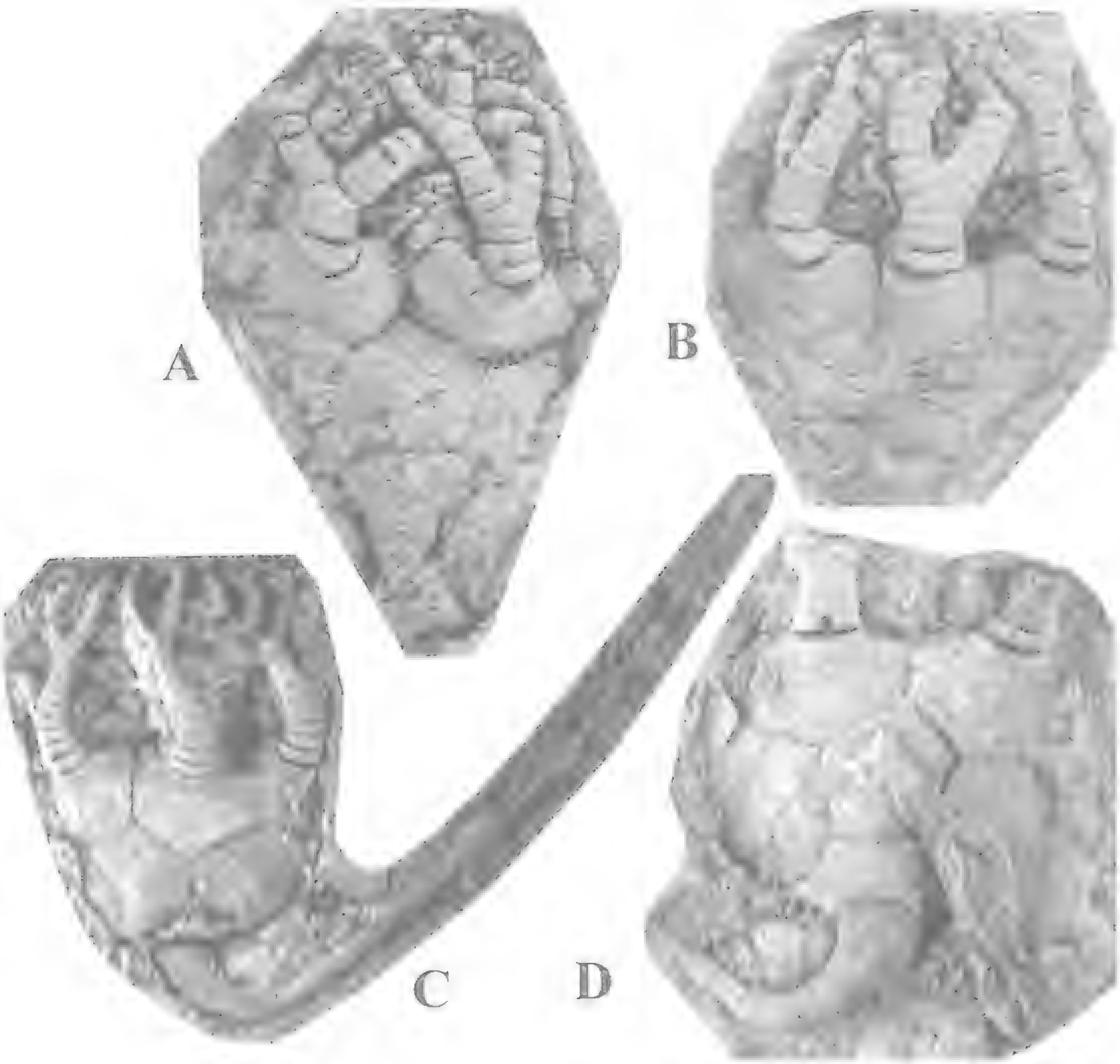



FIG. 55. *Codiacrinus secundus* sp. nov., all crowns in lateral view from NMVPL252. A,B, part and counterpart of NMVP108574, ×2.5. C, NMVP108576, ×2. D, NMVP108573, ×2.

subpentagonal section and the cirri are less regularly placed in *Crotalocrinites* and less nodular in *Syndetocrinus*. Nevertheless, there are striking resemblances in size, alignment of cirri in 5 vertical columns and external ornament of close-spaced horizontal grooves; on this basis it seems reasonable to make a family assignment. A crown of *Crotalocrinites pulcher* Hisinger, 1840 was recorded from the same rock unit in a white porous sandstone (Jell, 1982); it was collected from a gully where it had been placed by man and may have come from the same locality as these stem sections. On this basis I assign these distal stem segments to *Crotalocrinites* with the high probability that they belong to *C. pulcher*.

### Family CODIACRINIDAE Bather, 1890

### **Codiacrinus** Schultze, 1867

TYPE SPECIES. *Codiacrinus granulatus* Schultze, 1867 from the Eifelian of Germany near Prum; by original designation.

### **Codiacrinus secundus** sp.nov.
(Figs 55, 56)

ETYMOLOGY. Latin *secundus*, second; the second species of the genus recognised in Victoria.

MATERIAL. HOLOTYPE: NMVP108570. PARATYPES: NMVP108573, 108574, 108576, 108578, 108580, 108660, 109208, 109209, 149364 all from NMVPL252.

DIAGNOSIS. Cup finely granulose, with only the faintest suggestion of median ray ridges; radial facet occupying 1/2 radial width; first branching variable – 2nd, 3rd, 4th or 5th primibrach axillary;or peaks on the midline of the brachials absent; 1st secundibrachs and tertibrachs sutured against each other just distal to peak of axillary; stem tapering in proximal part, of short columnals separated by highly crenulate sutures.

DESCRIPTION. Crown subelliptical, 40mm long. Cup probably (always found flattened) of medium length, globose, with convex base; infrabasals 3, 2 large and 1 small, about half length of basals, forming pentagonal base to cup. Basals pentagonal, largest plates in cup, with extremely faint low median ray ridges forming central prominence and apparently in high cross meeting proximal and distal sutures at right angles. Rradials pentagonal, with low ray ridges continuing from basals to meet at midwidth of radial facet; radial facet less than half width of radial, almost circular (small tangential sector missing on oral side), sloping down and out only very gently (compression prevents accurate assessment but least disrupted specimen suggests virtually no slope), flat surface except for extremely weak transverse ridge almost disappearing medially, with fine canal emerging near outermost point on margin, with slightly raised rim around margin. Arms branching isotomously at least 3 times probably more; primibrachs usually with 4th axillary, one ray (Fig. 56F, left) with 2 primibrachs, quite short (diameter more than twice length), with same barely discernible transverse ridge as radial facet, with angular (70°-90°) projections orally beside wide shallow adoral groove; secundibrachs 5-7; tertibrachs 5; with 1st brachials in each arm above a fork sutured against each other for all or most of their length, with low nodes developed on the aboral midline of many secondary and distal brachials, with brachials increasing in length relative to diameter up the arms, with distal parts of arms curved back axially. Stem with very short, wide, highly crenulate columnals at base of cup, with columnal length increasing and columnal diameter decreasing away from cup, with long columnals in distal part of stem bearing circlet of stout rootlets; distal end of stem not preserved.

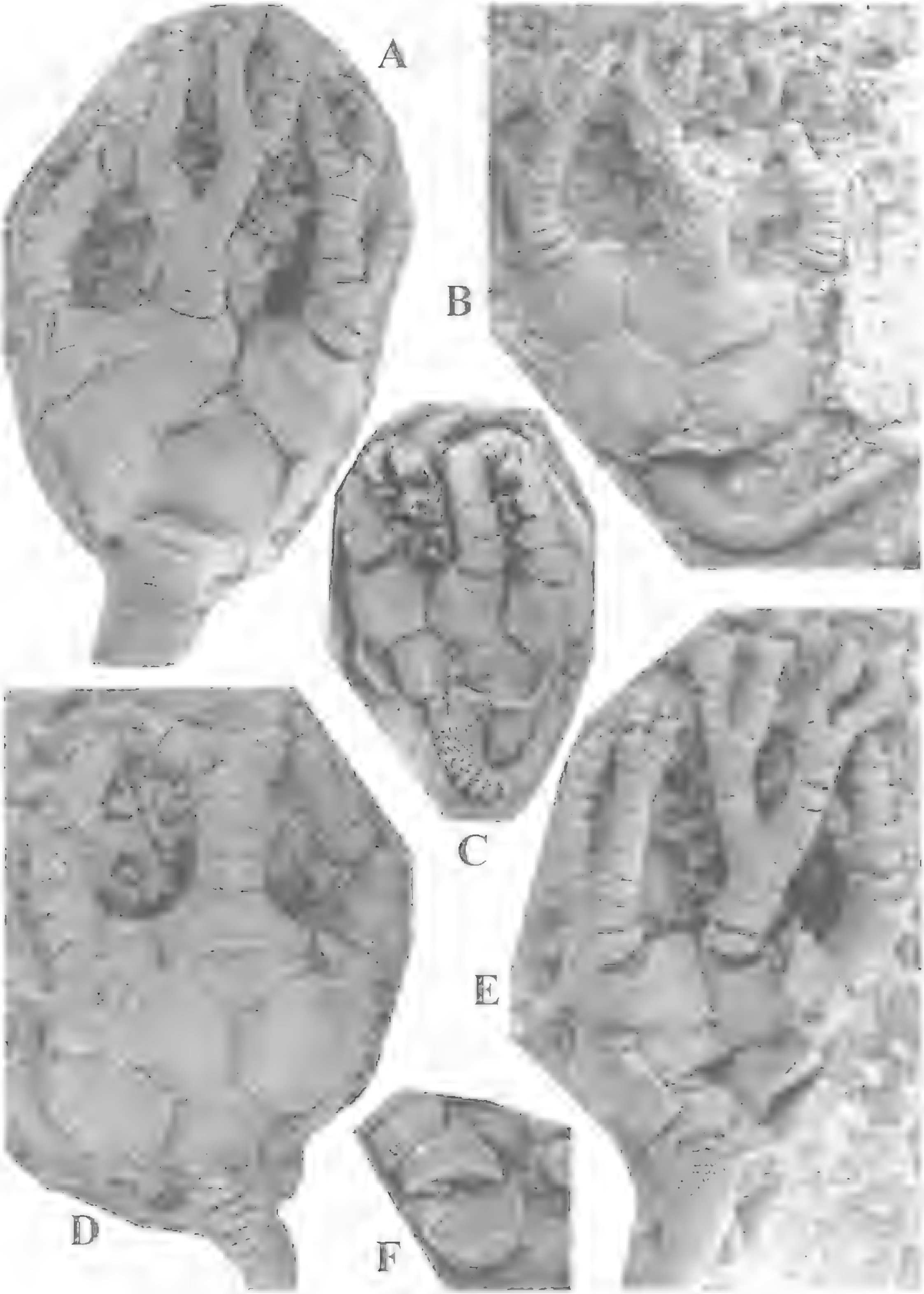
MORPHOGENY. One small individual (Fig. 56C) suggests that during growth the low ridges on cup plates became much less obvious, length of the basals increased relative to length of the radials from being less than in the small individual to being more than in large specimens, ratio of width to length of radials increased so making the cup more globose without introduction of new plates, and ratio of width to length of primibrachs and stem columnals increased dramatically.

REMARKS. This species is close to *C. schultzei* Follmann, 1887 from the Early Devonian Hunsrück Schiefer near Bundenbach, Germany, but is distinguished by its larger radial facets relative to size of radial plate, its variation in which primibrach is axillary, the suture between the 1st pair of brachials after an arm fork, by its nodes (if anything at all) rather than spines aborally on the midline of the brachials, and by the more tapering stem with shorter columnals. *Codiacrinus rarus* Jell in Jell & Holloway 1983 from the ?Early Devonian Humevale Formation at Winneke Reservoir may be distinguished by its narrower radials and consequently more conical cup, by its relatively higher infrabasals, and by its 1st brachials above arm forks not being sutured to each other. Czechoslovakian species *C. procerus* (Prokop,1973) and *C. ornatus* (Prokop, 1973) and the type species are all distinguished by their coarser granulose ornament among other features.

The variation in number of primibrachs in different rays of the same individual is unusual (Fig. 56F) and the ray with 2 primibrachs having 7 secundibrachs so that the 2nd forking takes place at the same level as in the adjacent ray with 4 primibrachs and 5-6 secundibrachs suggests some compensatory adjustment to arm growth.

This species is relatively common at NMVPL-252 but virtually every specimen is disrupted by plate dislocations making its shape difficult to establish and preventing any useful biometrics.

FIG. 56. *Codiacrinus secundus* sp. nov., all crowns in lateral view from NMVPL252. A, NMVP108660, ×1.9. B, NMVP108576, ×2.8. C, juvenile NMVP149364, ×4. D, NMVP108578, ×3.3. E, holotype NMVP108570, ×2.8. F, enlargement of distal articulating face of brachial NMVP108570, ×4.7.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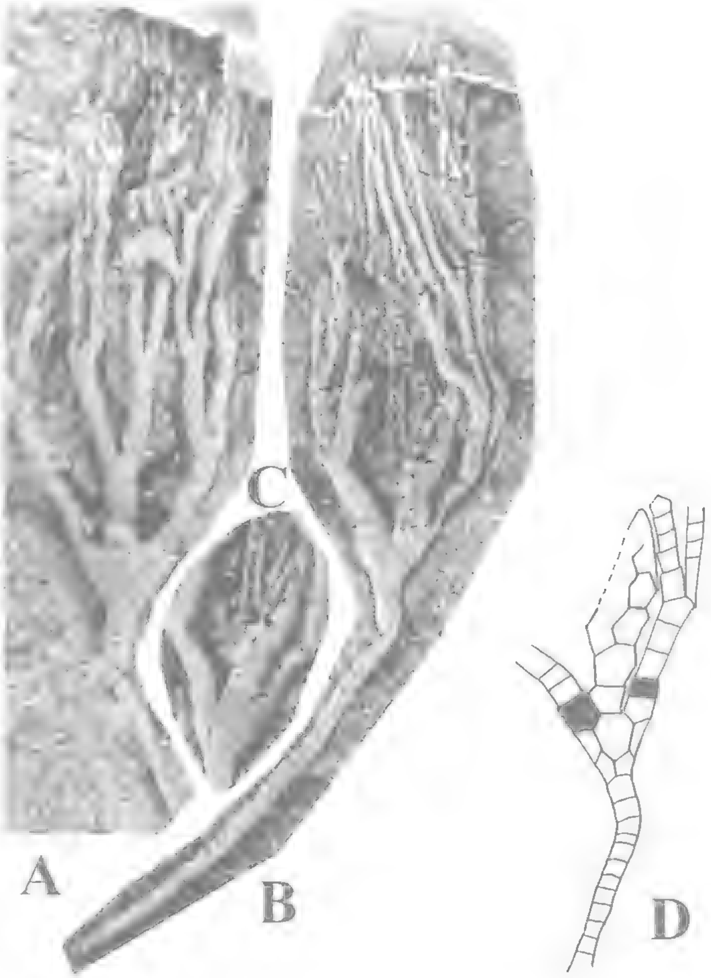



FIG. 57. *Cupulocrinus austrogracilis* sp. nov., holotype crown NMVP109194 from NMVPL1841, ×6. A, A ray view. B,C, posterior views. D, sketch of plate arrangement in posterior view.

Family CUPULOCRINIDAE
Moore & Laudon, 1943

**Cupulocrinus** d'Orbigny, 1850

TYPE SPECIES. *Scyphocrinus heterocostalis* Hall, 1847 from the Upper Ordovician of Canada; by monotypy.

REMARKS. Springer (1911) clarified the distinction between *Dendrocrinus* and *Cupulocrinus* based principally on the radial facet occupying all of the width of the radial in the latter but angustary in the former. Ramsbottom (1961) indicated a division within *Cupulocrinus* by noting that his Ashgillian species from Scotland are more similar to the type species than to North American species referred to the genus by Springer (1911). However, he did not indicate what features he used to make this division and no subsequent authors appear to have taken up this remark. Brower (1992) maintained the content of the genus with species as assigned except for *C. sepulchrum* Ramsbottom, 1961 (moved to *Dendrocrinus*) and *C. conjugans* for which he erected *Praecupulocrinus*. Despite this well expressed generic concept the 2 new Australian species which comply with the generic diagnosis are so different, that assessment of Ramsbottom's (1961) inference for further subdivision is necessary. The other problem with the Australian species is their geographic and stratigraphic separation. In the absence of any Silurian forms I am very dubious about assignment to this previously Ordovician genus. However, *C. austrogracilis* is so similar to *C. drummuckensis* Kolata, 1975 (=*C. gracilis* of Ramsbottom, 1961) that it is difficult to diagnose them effectively. Given the isolation of this Australian species I am very loathe to credit a genus with such an unusual range and distribution, but there is no morphological basis for excluding it from *Cupulocrinus*. The second Australian cupulocrinid is separated as *Stewbrecrinus* gen. nov. below.

**Cupulocrinus austrogracilis** sp. nov.
(Fig. 57)

ETYMOLOGY. Latin *australis*, southern and *gracilis* slender, also referring to it being southern version of *C. gracilis*.

MATERIAL. HOLOTYPE: NMVP109194 from NMVPL1841.

DIAGNOSIS. Crown 15mm long, subcylindrical. Cup low conical, moderately flared distally, with straight to slightly concave sides. Infrabasals short (1/4 or less of cup length), tapering proximally. Arms long and slender. Stem very slender, of uniform, relatively long, barrel-shaped columnals.

DESCRIPTION. Crown small, 14mm long. Cup 1.4mm long, conical, maximum width distally on radials 2mm. Thecal plates smooth. Infrabasals pentagonal, very short, upflared (not well defined on the specimen). Basals 5, hexagonal except for heptagonal CD basal, about as long as wide. Radials 5, pentagonal, as long as wide, largest plates in cup; radial facet plenary. Radianal pentagonal, in inferradial position proximal to C radial; anal X resting directly on CD basal, reaching almost to top of D radial and about halfway up C radial, supporting single large hexagonal anal leading into vertical column of similarly shaped plates decreasing in size distally. Arms isotomous, narrow, dividing 3 times on 4th primibrach, 3rd to 5th secundibrach and on various tertibrachs, 3rd divisions in same arm at same height, uniserial, nonpinnulate, with rectangular brachials throughout. Stem circular in section, of uniform barrel-shaped columnals.

REMARKS. This species is very similar to *C. gracilis* from the Middle Ordovician of North America (Kolata, 1975) particularly in structure of the posterior interray and even to relative size shape and plating of the anal tube, but differing only in the stem, height to width ratio of brachials and ratio of stem diameter to maximum cup diameter.

## **Stewbrecrinus** gen. nov.

TYPE SPECIES. *Stewbrecrinus terryi* sp. nov.

ETYMOLOGY. An anagram from Webster plus the usual suffix for crinoids; for Gary Webster who has contributed greatly to Australian crinoid studies.

DIAGNOSIS. Cup dicyclic, usually expanding distally, with base of small to medium diameter. Radials usually wider than long, with radial facet plenary. Radianal in inferradial position proximal to C radial. Anal X very large, supporting a single large anal plate. Interprimibrachs small, irregular, numerous. Arms 5, uniserial, nonpinnulate, dividing isotomously at least 3 times, with primibrachs of more or less uniform width, with distinct patelloid processes at least in primibrachs. Stem heteromorphic, with nodals circular in section, with internodals decagonal.

REMARKS. Although this species satisfies the criteria for *Cupulocrinus* and is very closely

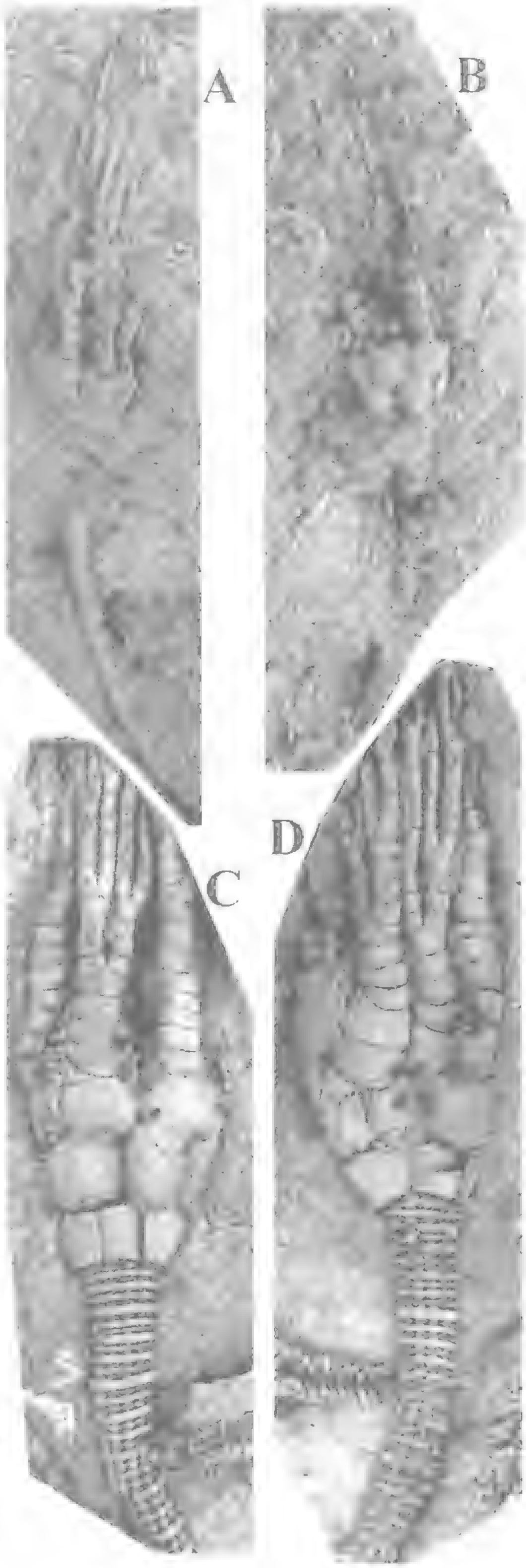



FIG. 58. *Stewbrecrinus terryi* gen. et sp. nov., crowns from NMVPL1924. A,B, part and counterpart of juvenile NMVP109766, ×1. C,D, part and counterpart of holotype NMVP109215, ×2.2.

allied to a few species of that genus its geographic and stratigraphic separation prompts me to allocate generic status. If in the future a lineage is found to link these species at least 2 species now assigned to *Cupulocrinus* could move to *Stewbrecrinus*. The new Australian Devonian genus may be distinguished from *Cupulocrinus* and *Praecupulocrinus* by its stem structure, by its curved rather than straight horizontal suture between radial and 1st primibrach and by the juvenile radial facet being much narrower than the radial plate. Brower (1992) showed in the species he erected that the radial facet occupies the full width of the radial even in the juvenile stage. However, growth series are not available for most species. The small interbrachial plates in the holotype of *S. terryi* may be a feature that indicates a generic grouping and if species with interbrachials are found in the Silurian the content of *Stewbrecrinus* may include Ordovician *C. humilis*, and *C. jewetti* (Springer, 1911).

**Stewbrecrinus terryi** sp. nov.
(Fig. 58)

ETYMOLOGY. For Terry Brady who helped collect crinoids at Kinglake West.

MATERIAL. HOLOTYPE: NMVP109215. PARATYPE: NMVP109766 from NMVPL1924.

DIAGNOSIS. As for genus.

DESCRIPTION. Crown subcylindrical, 30mm long, with arms more than twice as long as cup. Cup high conical, with basal diameter more than half summit diameter, dicyclic; plates smooth. Infrabasals 5, pentagonal, slightly longer than wide, with very high obtuse angle between 2 upper sides. Basals 5, hexagonal, as wide as long; CD basal larger than others, with 7 sides, supporting anal X symmetrically distal to it; anal X large, extending above radials, supporting one large anal plate medially over most of width of anal X and many tiny plates lateral to it. Radials 5, pentagonal except C radial subquadrate; radial facets angustary in small individual becoming plenary in large specimen, declivate, with evenly downcurved suture to 1st primibrach. Radianal pentagonal, in inferradial position proximal to C radial and separated from it by straight horizontal suture. Arms 5, branching isotomously at least 3 times, uniserial, nonpinnulate, with patelloid processes; primibrach 4 axillary except in D ray where 5th primibrach axillary; secundibrach 4 axillary; tertibrach 5 or 6 axillary. Stem heteromorphic, tapering slightly distally in most proximal part, circular in overall section, noditaxis N212, with internodals having serrated latus, tapering slightly over proximal 1cm.

REMARKS. This species is distinguished by its stem, its curved suture between radial and 1st primibrach and by its interbrachial plates.

The holotype is slightly crushed so that interradial areas between A, B and C rays are obliterated and anal X has ridden out over C radial. The interbrachial plates are only clear in the EA interradius; some are evident deep within the DE interradius. The edge of the anal X against the D radial is projected straight out of the surface of the latex just above the D radial and between it and the 1st primibrach of the D ray are a number of tiny plates suggesting strongly that a median column of large plates is laterally attended by fields of tiny plates; such plating of the anal interarea would align perfectly with that of *Cupulocrinus humilis* and *C. jewetti* as illustrated by Springer (1911). The numerous pits randomly distributed over the holotype cup and proximal primibrachs are interpreted as borings effected by another unknown organism.

Order DENDROCRINIDA Wachsmuth & Springer, 1886
Family DENDROCRINIDAE Wachsmuth & Springer, 1886

**Dendrocrinus** Hall, 1852

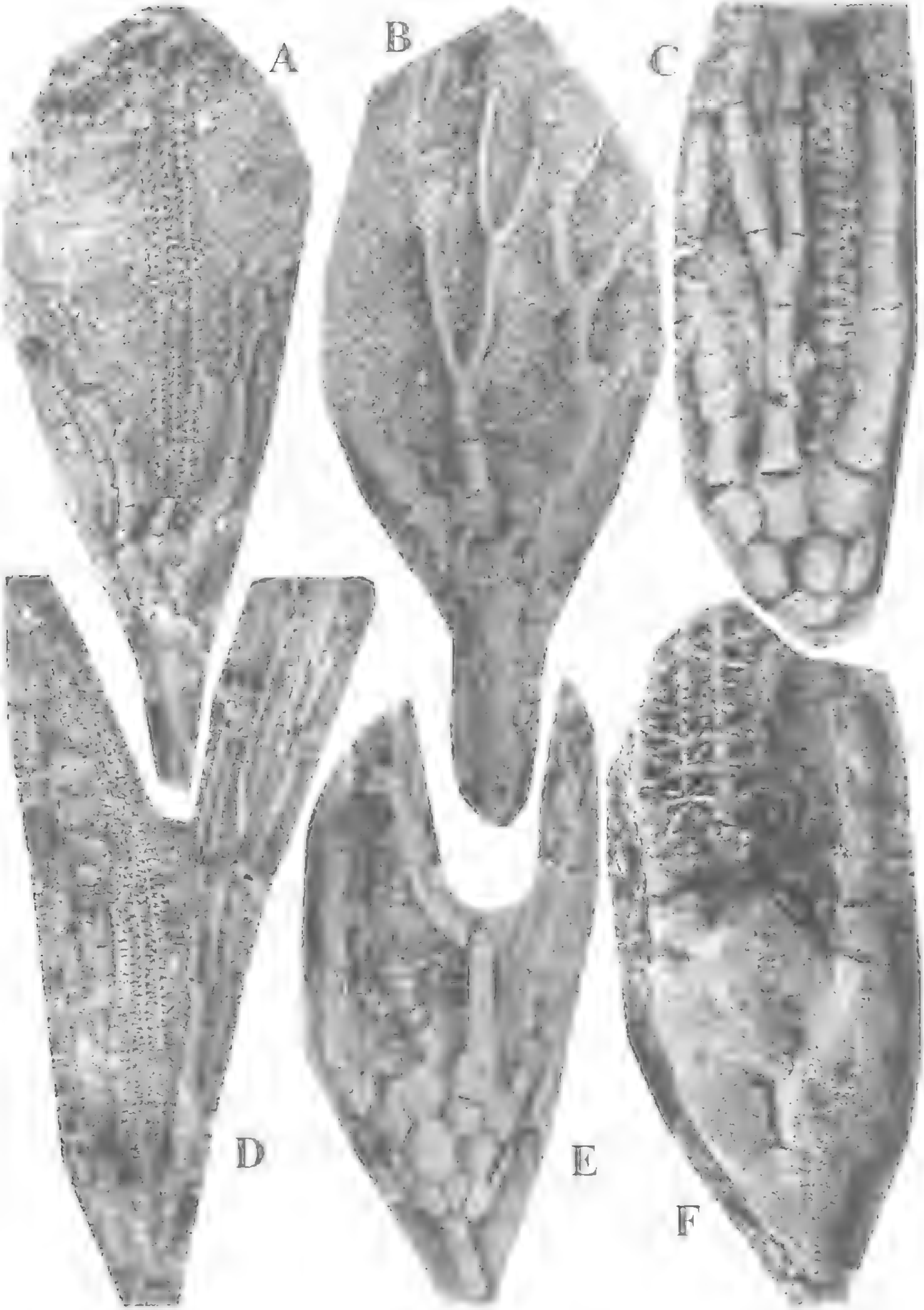
TYPE SPECIES. *D. longidactylus* Hall, 1852 from the Wenlock of New York; by original designation.

**Dendrocrinus arrugius** sp. nov.
(Figs 59-63)

ETYMOLOGY. Latin *arrugia*, a mine; from the vicinity of Comet Creek Mine.

MATERIAL. HOLOTYPE: NMVP109774. PARATYPES: NMVP109119, 109781, 109786, 109788-109790, 109802, 109813, 109823, 110630, 149365 all from NMVPL300 (Ludlow). OTHER MATERIAL: NMVP109187 from SW side of Bald Hills, NE of Kilmore; NMVP112133, 112137, 112138, 112140 and 112141 from NMVPL1925 (Ludlow). DOUBTFUL MATERIAL: NMVP108619, 149358 from NMVPL252 (Lochkovian).

FIG. 59. *Dendrocrinus arrugius* sp. nov., all crowns in lateral view from NMVPL300. A, anterior view of NMVP109813, ×3.5. B, NMVP109823, ×4. C, NMVP109790, ×4. D, posterior view of NMVP149365, ×1.5. E, posterior view of NMVP109781, ×3. F, C ray view of NMVP110630, ×3.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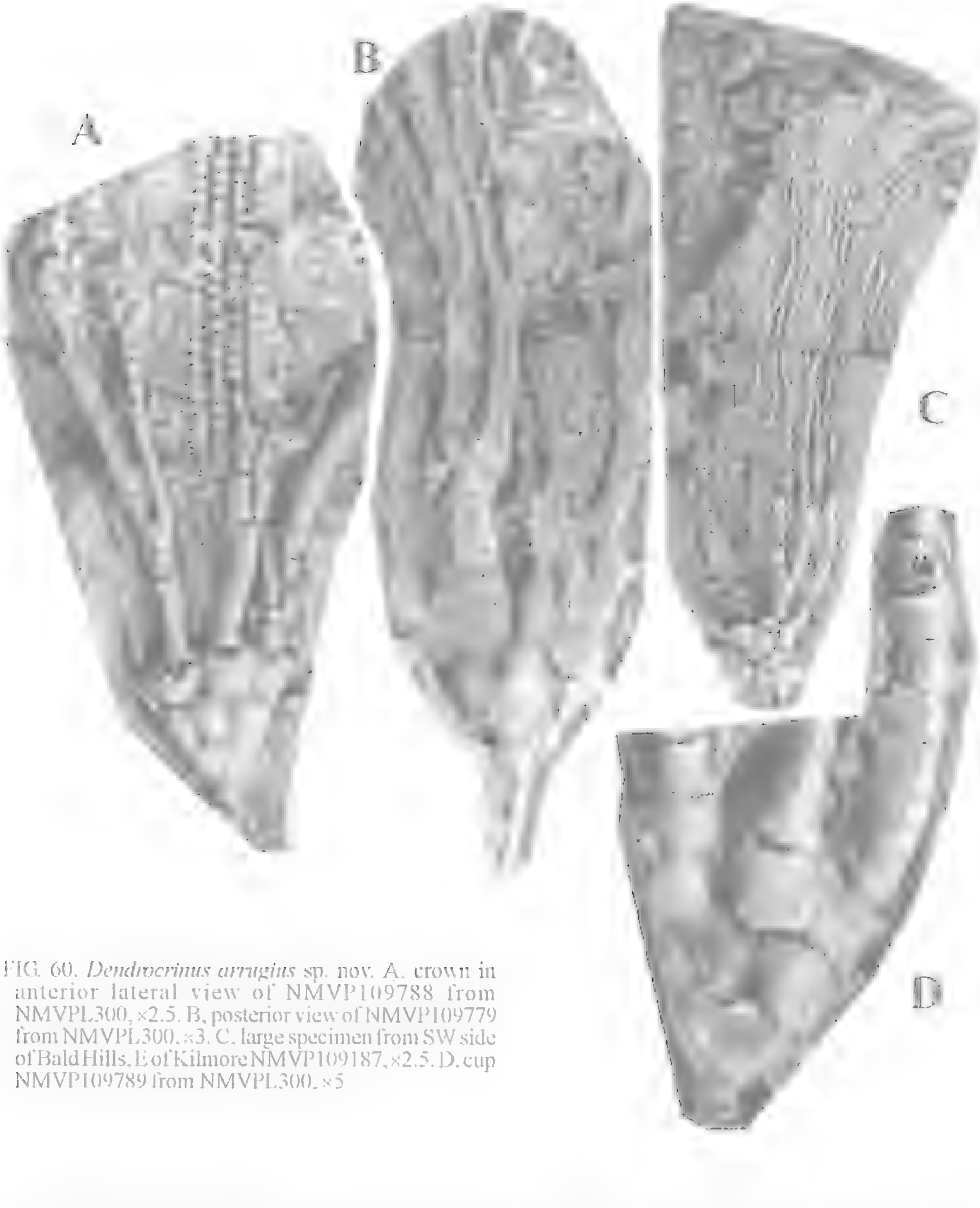
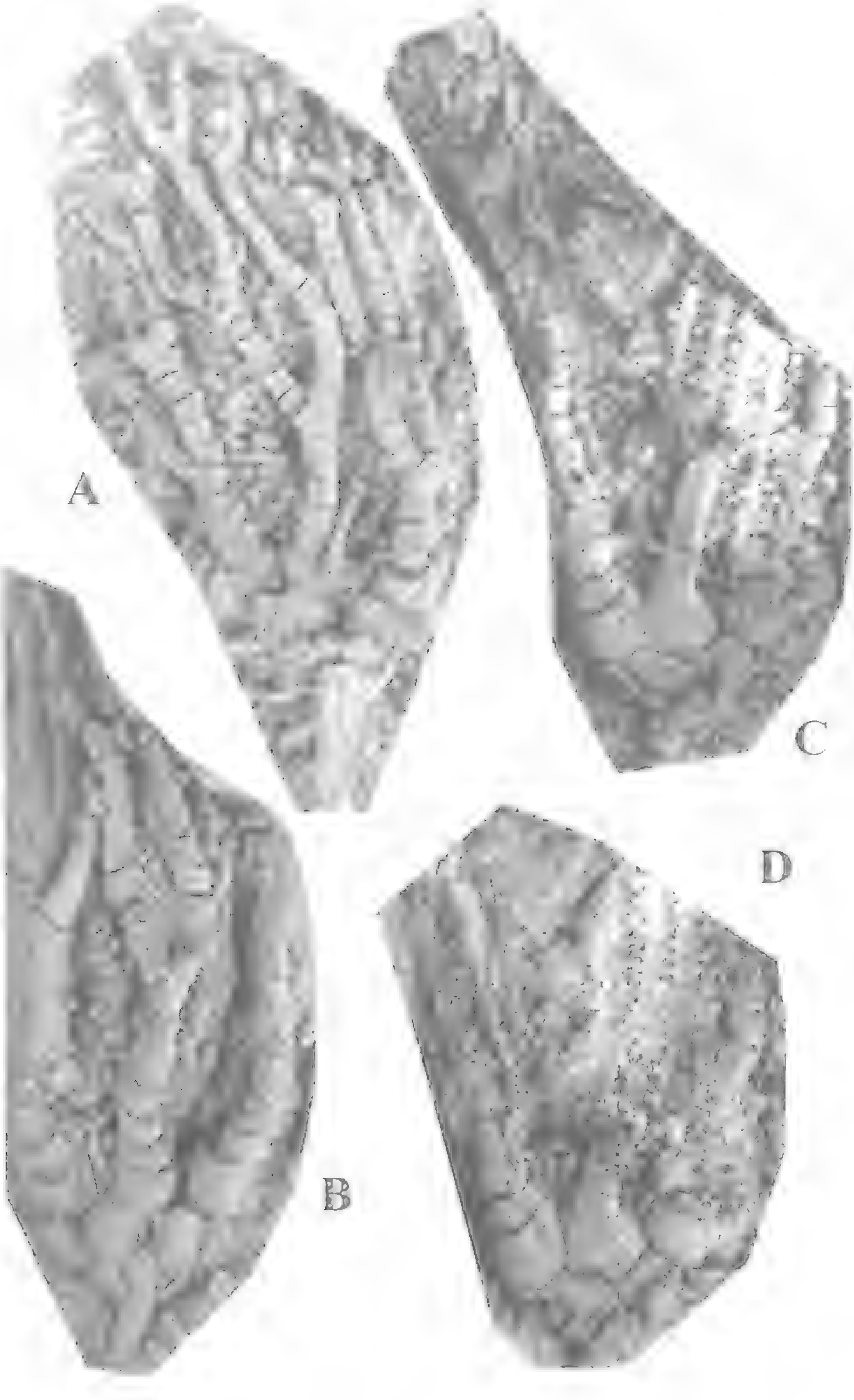



FIG. 60. *Dendrocrinus arrugius* sp. nov. A, crown in anterior lateral view of NMVP109788 from NMVPL300, ×2.5. B, posterior view of NMVP109779 from NMVPL300, ×3. C, large specimen from SW side of Bald Hills, E of Kilmore NMVP109187, ×2.5. D, cup NMVP109789 from NMVPL300, ×5

FIG. 61. A, C, D, ?*Dendrocrinus arrugius* sp. nov. A, crown in anterior view NMVP108619 from NMVPL252, ×3.C,D, D ray view of incomplete crown with successive latex pulls from same specimen showing exterior (C) and interior (D) of anal tube of NMVP149358 from NMVPL252, ×3. B, *Dendrocrinus arrugius* sp. nov.crown in anterior view NMVP109786 from NMVPL300, ×3.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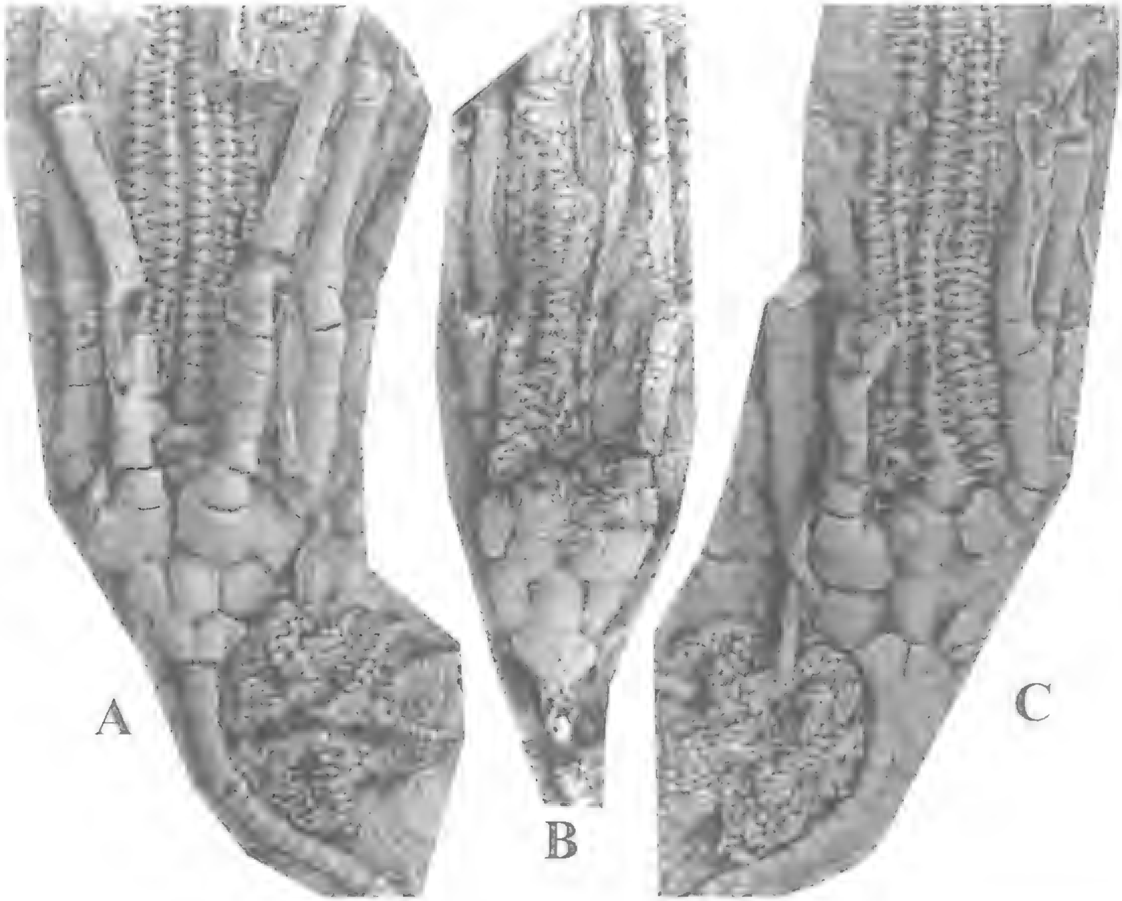
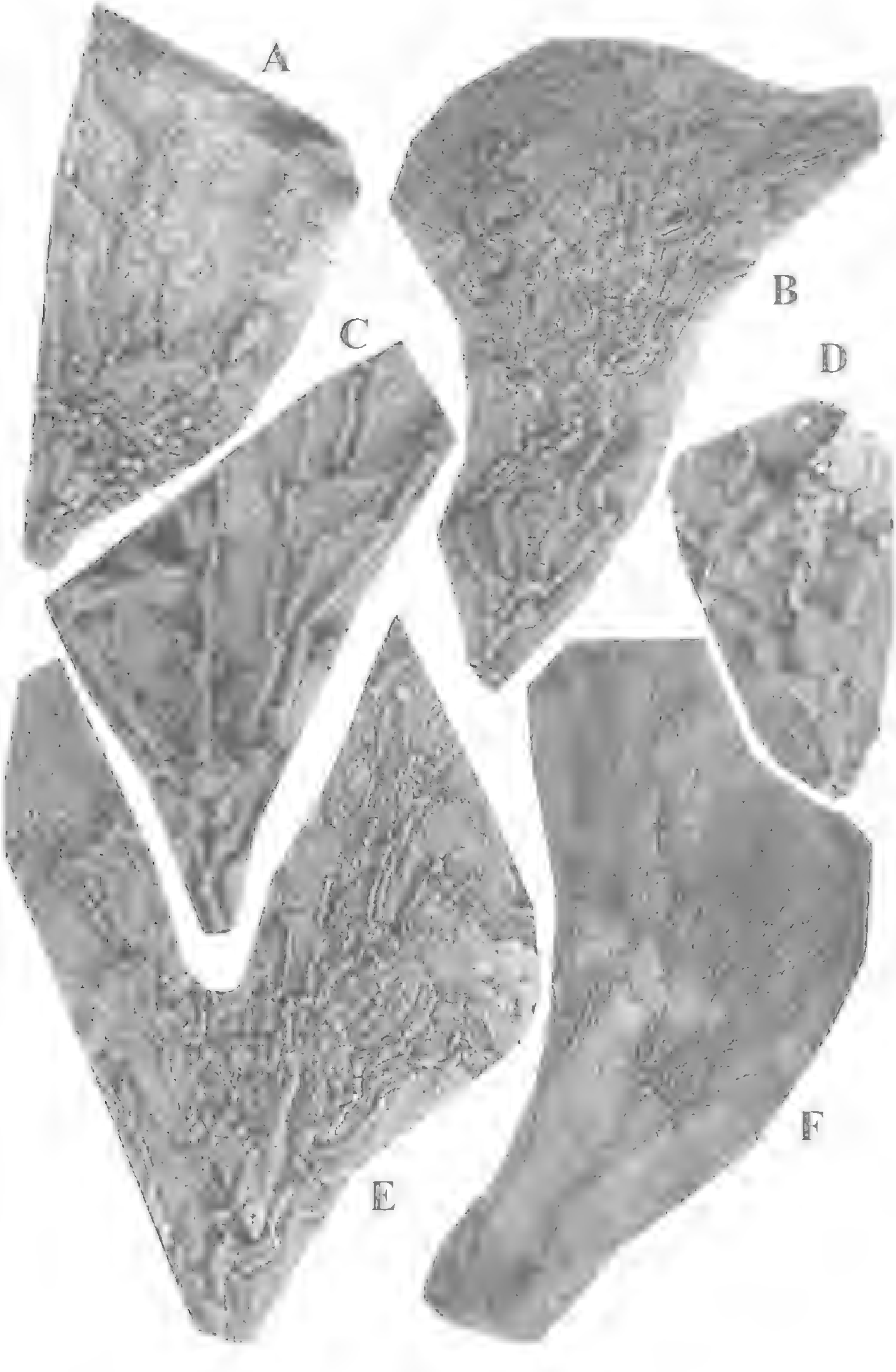


FIG. 62. *Dendrocrinus arrugius* sp. nov. A,C, part and counterpart of holotype crown with small asterozoan at base of NMVP109774 from NMVPL300, ×2.5. B, crown in C ray view of NMVP109790 from NMVPL300, ×3.

DIAGNOSIS. Crown subcylindrical to evenly subconical, 75mm long, with anal tube longer than arms. Cup plates thin, smooth except for ray ridges variably expressed from specimen to specimen. Radianal pentagonal, in inferoradial position beneath C radial. Radial facet occupying 3/4 or more of radial width, circular, gently declined. Anal X supporting 3 anals becoming plicate and succeeded by very tall plicate anal tube. Arms uniserial, isotomous, branching 5 or more times, nonpinnulate. Stem very narrow, circular in section, noditaxis N1, with longer nodals projecting slightly laterally.

DESCRIPTION. Crown very long, almost 10 times as long as maximum cup width, with anal tube extending well beyond arms. Cup conical, moderately long and flared, length about equal to maximum width. Thecal plates thin, smooth, with depressed corners in some specimens, with ray ridges well-developed on some specimens (particularly on radials). Infrabasals 5, pentagonal, longer than wide, tapering strongly proximally, with high obtuse angle between upper 2 sides, fully visible laterally except for basal flange against top of stem. Basals 5, hexagonal, longer than wide; posterior basal 7-sided, supporting anal X distally. Radials 5, hexagonal, with distal 2 sides angling up inside the radial facet; radial facet occupying 3/4 or more of radial width, circular, gently declined outwards, with

FIG. 63. *Dendrocrinus arrugius* sp. nov. all crowns from NMVPL1925. A, NMVP112140, ×1.8. B, NMVP112137, ×1.8. C, NMVP112133, ×1.8. D, NMVP149359, ×1.8. E, NMVP112138, ×1.8. F, NMVP112141, ×0.9.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weak transverse ridge. Anal plates in cup 2: anal X large, 6-sided, as long as wide, in radial circlet, on same level as C radial but slightly longer than D radial; radianal, pentagonal, in inferradial position proximal to C radial from which it is separated by a horizontal suture. Anal sac longer than arms, straight, of 10 vertical columns of plicate plates. Arms narrow, circular to deep U-shaped in section, with deep V-sectioned furrow on inside covered by small cuneate coverplates, isotomous, dividing 5 or more times, with primibrach 5 axillary (6 in A ray), secundibrach 8 axillary. Stem circular in section, heteromorphic, with nodals longer and of slightly greater diameter than internodals.

REMARKS. The only record of *Dendrocrinus* from Australia (*D. saundersi* Jell in Jell & Holloway, 1983) is possibly the youngest record of this essentially Ordovician genus globally, coming from near the Silurian/Devonian boundary. Ludlow species are apparently unknown but the type species is from the Wenlock of New York. This new species from the Ludlow helps to link *saundersi* back to the bulk of the genus. As with my discussion of *D. saundersi* many of the Northern Hemisphere species remain difficult to compare because they have not been revised this century. Nevertheless, it appears the plicate ornament on the very long anal tube beginning on the 1st anal distal to anal X, broader radial facets, radianal in inferradial position and low ray ridge ornament separate this from known species of the genus including the type which also has quite large lower anal plates filling the entire interray. *D. saundersi* has a smooth slender anal tube, fewer branches in the arms and more obviously beaded stem.

Material assigned to this species from NMVPL1925, in Dry Creek adjacent to the railway line under the bridge on Saunders Road, E of Kilmore, has a markedly different appearance to that from NMVPL300 to the SE. The NMVPL-1925 matrix has a fine crinkly cleavage and as the locality is close to a fold axis (Vandenberg, 1992) within the Kilmore East Synclinorium I suggest that a lot of the sharp angle bends in some cup plates are due to this cleavage. Depending on their orientation to the tectonic forces some specimens have been shortened others have been elongated and narrowed. However, the very long plicate anal tube (Fig. 63A,E) and the radianal symmetrically below C radial (Fig. 63D) along with the nature of the stem and numerous arm branchings are sufficient to be confident of the identification.

FIG. 64. *Dendrocrinus* sp. B ray view of cup NMVP100491 from NMVPL1927, ×3.

Two specimens from NMVPL252 in the Lochkovian are very tentatively referred to this species even though only the anterior is available. The more complete specimen (Fig. 62A) matches extremely closely, typical specimens from NMVPL300 (Fig. 62B). In the Devonian specimen the stem appears wider relative to the cup and what appears to be the anterior of the anal tube running from between the A and B radials to about 11 o'clock beneath the arms lacks the plicate ornament. However, the second specimen from the same locality clearly shows the plicate ornament. There are no other known species from NMVPL252 to which these specimens could be assigned unless they represents a new taxon. Therefore we make very doubtful assignment to *D. arrugius* fully aware that this would infer an extremly longranging species, Ludlow to Lochkovian. A number of other species do have this range in the Melbourne Trough sedimentary structure.

**Dendrocrinus** sp.
(Fig. 64)

MATERIAL. NMVP100491 from NMVPL1927 at the crossing of Broadhurst Creek by the Kilmore to Wandong Road.

DESCRIPTION. One side of cup (A-C rays only) preserved; cup low, conical, of smooth thin plates with broad low median ray ridges. Infrabasals 5, pentagonal, more or less equidimensional, with proximal margin projecting out medially. Basals

5, hexagonal, longer than wide; A-B basal with straight horizontal suture dividing it into 2 pentagonal plates. Radials 5, pentagonal except B radial with an extra side against radianal and C radial with one less side because of horizontal base against radianal, with low indistinct radial ridges emanating from centre just below radial facet angustary, only gently declivate. Radianal only anal plate available, pentagonal, in inferradial position proximal to C radial, separated by horizontal suture, with low ridge running proximally from C radial and dividing near midlength and continuing onto basals. Arms 5, deep U-shaped in section, with deep V-shaped groove on inner side, apparently isotomous, with 3rd primibrach axillary. Stem unknown.

REMARKS. This specimen is too incomplete to provide a full species concept but it has some features that make it unique. It is the only crinoid from this horizon. The radianal in inferradial position proximal to the C radial identifies it as *Dendrocrinus*. The divided AB basal is unknown in any other cladid: it could be an aberrant specimen, which I consider most likely or it could be the last remnant of a 4th circlet of cup plates that may have been in its ancestry. The latter possibility suggests derivation from *Aethocrinus* as suggested by McIntosh (1983).

## Family PLICODENDROCRINIDAE nov.

DIAGNOSIS. Cup low to high conical; thecal plates with narrow, radial ridges; infrabasals 5; radial facets poorly developed, transverse ridge usually absent but when present bisected by prominent V-shaped ambulacral groove; 2 or 3 anal plates in cup; rarely with inferradianal; radianal either pentagonal and in inferradial position or quadrangular; arms usually isotomous, rarely heterotomous; outer faces of proximal brachials mostly angular; anal sac straight, inflated, of thin plicate plates.

GENERA ASSIGNED. *Plicodendrocrinus* Brower, 1995 (Upper Ordovician (Ashgill); central USA). *Compagicrinus* Jobson & Paul, 1979 (Lower Ordovician (Arenig); northern Greenland). *Holmesocrinus* gen. nov. (Silurian (Ludlow); central Victoria).

REMARKS. The concept of this family was first documented in an unpublished thesis by George McIntosh (1983) and when he refereed this paper he insisted that I name the family from this date upon which I insisted that I acknowledge the origin of the concept. McIntosh (1983) separated *D. casei* from *Dendrocrinus* as type of a new genus and used that genus as the type of a subfamily of the Dendrocrinidae including *Compagicrinus* and a new genus based on *Botryocrinus reimanni* Goldring, 1934 from the Middle Devonian of New York.. Thus when Brower (1995) established *Plicodendrocrinus* with *D. casei* as type species he endorsed McIntosh's generic concept but with a different name. It was the group of species now asigned to *Plicodendrocrinus* that Jobson & Paul (1979) had in mind when they showed *Compagicrinus* giving rise to *Dendrocrinus*. Their figure would now be modified to show the Plicodendrocrinidae continuing on beyond the Middle Silurian and a parallel arrow for the Dendrocrinidae which has very similar stratigraphic range. McIntosh's subfamily concept remains in tact and now takes its name from Brower's genus. In this paper I employ McIntosh's subfamily concept at family level because with the description below of Ludlow and Lochkov members it is clear that the lineage continued from the Lower Ordovician through the middle Palaeozoic independent of *Dendrocrinus* and although it may contain the ancestor of the Dendrocrinidae that is a recognisably distinct lineage that should be treated as such. The diagnosis used here is McIntosh's with minor modification to accept the Australian genus.

### **Plicodendrocrinus** Brower, 1995

TYPE SPECIES. *Poteriocrinites (Dendrocrinus) casei* Meek, 1871 from the Upper Ordovician of USA; by original designation.

DIAGNOSIS. Two anal plates in cup; inferradianal absent; superradianal pentagonal, in inferradial position proximal to C radial. Anal sac inflated, elongate, of staggered columns of strongly plicate plates proximally, with numerous (20-30) randomly arranged sets of sac plates distally. Arms isotomous, non-pinnulate; proximal brachials angular or cuneiform, with distinct cornice-like flaring in distal direction. Stem pentastellate or decagonal to round, lacking pentameres.

INCLUDED SPECIES. The type, *Dendrocrinus grandituhus* Ramsbottom, 1961, *D. rugocyathus* Ramsbottom, 1961, *Dendrocrinus proboscidiatus* Billings, 1857 and *P. australis* sp. nov.

### **Plicodendrocrinus australis** sp. nov. (Figs 65B-E, 66B)

ETYMOLOGY. Latin *australis*, southern.

MATERIAL. HOLOTYPE: NMVP100191. PARATYPE: NMVP112129 from NMVPL252.

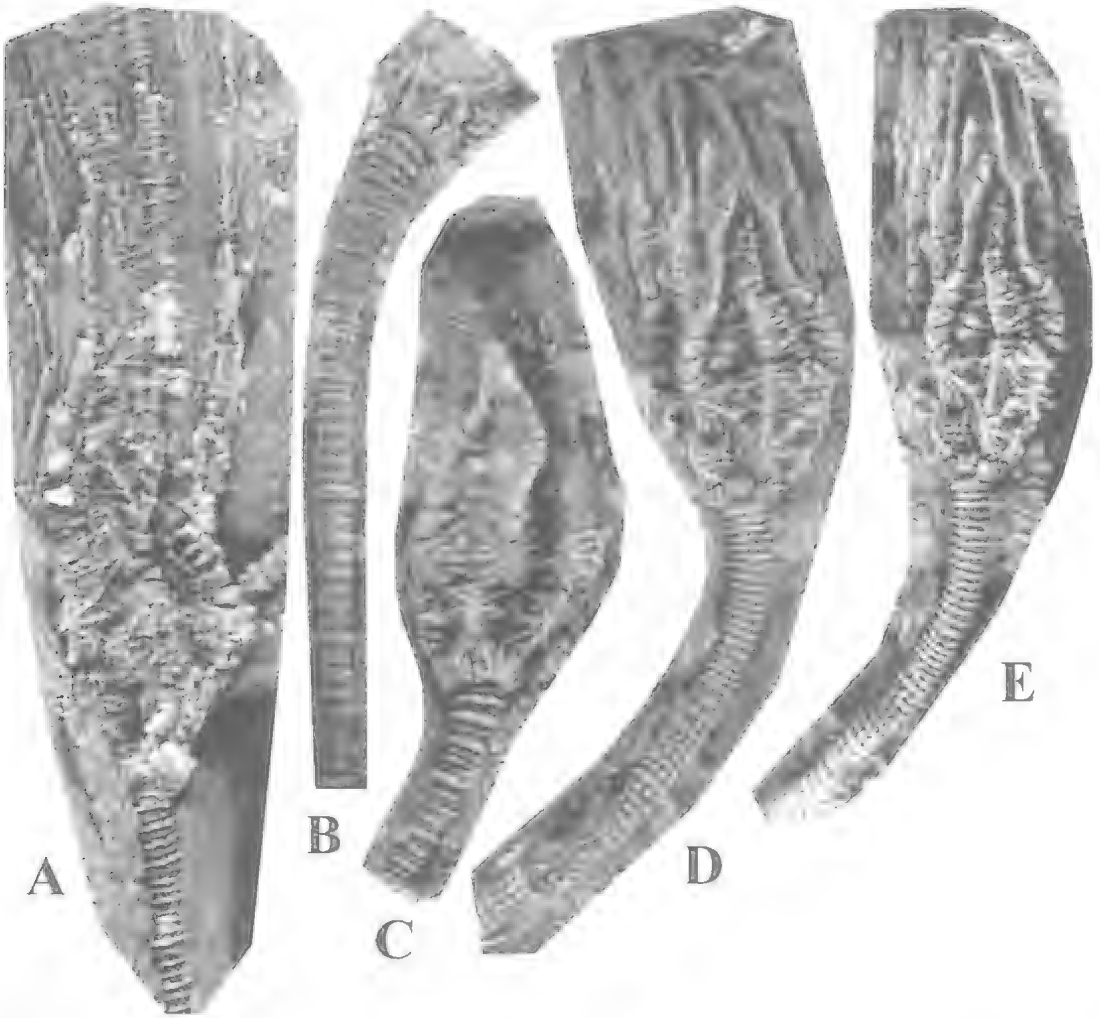



FIG. 65. A, *Shintocrinus richi* sp. nov., posterior view of crushed crown of holotype NMVP149390 from NMVPL1990, ×2.5. B-E, *Plicodendrocrinus australis* sp. nov. B,C, part and counterpart of crown (B stem and infrabasal circlet only) NMVP112129, ×2. D,E, D ray and posterior views of holotype crown NMVP100191, ×3.

DIAGNOSIS. Thecal plates with low, narrow radial ornament and fine subsidiary interradial ridges parallel to the radial ridges; radial facet narrow relative to radial width; 4th primibrach axillary; arms isotomous, dividing at least 3 times. Stem decagonal, round proximally, with distinct nodals and internodals becoming less differentiated distally.

DESCRIPTION. Crown subcylindrical, 15mm long. Cup low, conical, wider than long. Thecal plates, thin, prominently ornamented with vertical (on radials and posterior interray), horizontal (on radials and basals) and diagonal (on all plates) ridges continuous from plate to plate; major ridges at right angles to interplate sutures, radiating from just below facet on radials, from middle of basals, radianal and anal X and from midpoint of proximal margin against stem on infrabasals; secondary ridges between main ridges running to corners of plates. Infrabasals 5, pentagonal, as wide as long, smallest plates in cup, upflared, visible in lateral view except for bases resting on stem. Each infrabasal with 3 ridges originating from centre of base; 2 run diagonally onto adjacent basals, 3rd vertical to upper corner not extending further. Basals 5, hexagonal, largest plates in cup, longer than wide, with central elevated point as origin of 6 major ridges continuous onto contiguous plates

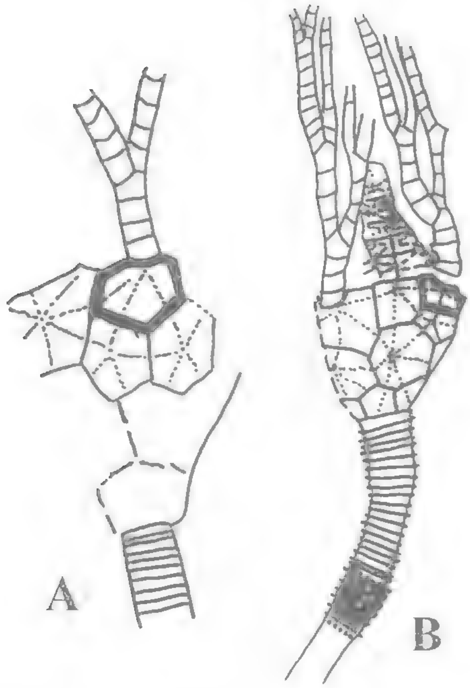



FIG. 66. Sketches of holotypes to show posterior plating (C radial heavily outlined). A, *Shintocrinus richi* sp. nov., B, *Plicodendrocrinus australis* sp. nov.

at right angles to interplate sutures, with secondary ridges running to plate corners not always originating at centre; posterior basal 7-sided and with 7 major ridges, with 3 distal riges running to D radial, anal X and radianal. Radials 5, pentagonal, width about equal to length, with 6 major ridges radiating from centre just proximal to facet, with 2 horizontally to adjacent radials, 2 diagonally to basals and 2 diagonally to distal corners of radial distal to facets. Radial facets angustary, U-shaped, just distal to midlength of radial. Two anal plates in cup; radianal pentagonal, in inferradial position proximal to C radial, with 5 main ridges radiating from centre to contiguous plates; anal X large, symmetrically distal to CD basal in radial circlet, with 7 main ridges radiating from the centre, with asymmetrical ridge diagonally to radianal. Anal sac long, composed of columns of plicate plates, with strong vertical ridge on posterior midline. Arms isotomous, non-pinnulate, narrow and deep giving high U-shaped section with angular outer margin, bifurcating on 4th primibrach, 4th secundibrach and 7th tertibrach. Stem decagonal (most noticeable in internodals) in section, consisting of alternating nodals and internodals, markedly heteromorphic in proximal part of stem but almost uniform distally.

REMARKS. This species is most simply distinguished from the other 5 species, all from the Ordovician of the Northern Hemisphere, by its decagonal to rounded stem but also by its finer, more elaborate thecal plate ornament. Although the holotype cup is crushed the central peak of the radianal and the C radial are in a vertical line to confirm this dendrocinid feature. Although the upper extension of the anal sac is not available it does not seem likely, from the arms closing around the sac in the holotype, that it is so prominently expanded as it is in *P. grandituhus*. *P. rugocyathus* is distinguished by the coarse radial ornament on thecal plates.

### **Shintocrinus** gen. nov.

TYPE SPECIES. *Shintocrinus cometensis* sp. nov.

ETYMOLOGY. An anagram from Intosh, for George McIntosh of the Rochester Museum.

DIAGNOSIS. Two anal plates in cup; radianal subquadrate to pentagonal; anal sac inflated, of 8 staggered rows of plicate sac plates; arms isotomous; proximal brachials angular, with distinct cornice-like flaring; stem round.

INCLUDED SPECIES. The type, *S. richi* sp. nov. and possibly *S. costatus* (Angelin, 1878) (i.e. *Pycnosaccus scrobiculatus* in part of Springer, 1926, pl. 11, fig. 10).

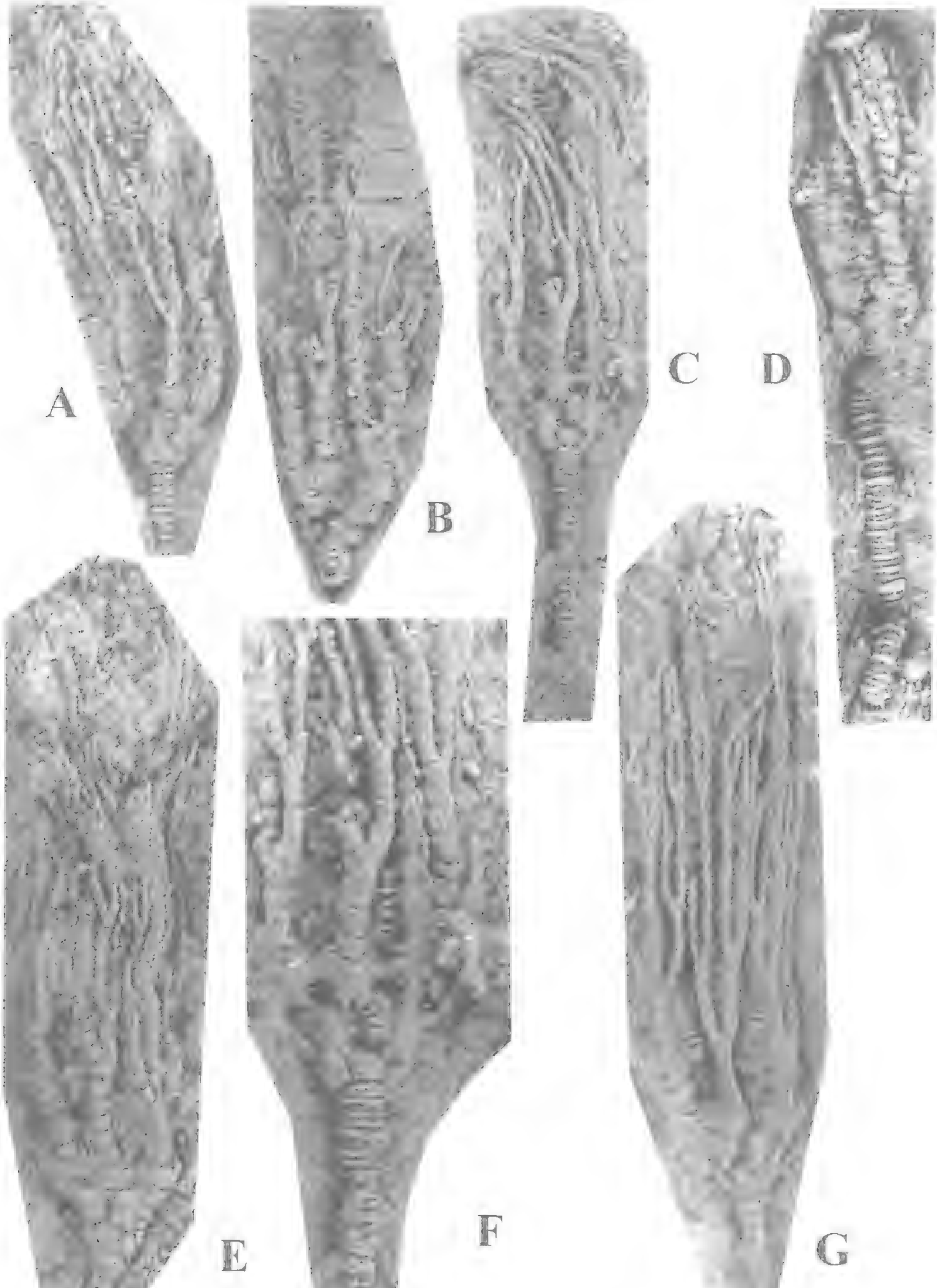
REMARKS. This genus shares with *Plicodendrocrinus* its isotomous arms, its conservative radial facets, thin cup plates and straight anal tube but differs from it principally by the position of its radianal, by its arms branching only 3 times and round stem. *Shintocrinus* differs from *Holmesocrinus* in the nature of the stem, slightly different position of the radianal (more to left of C radial than inferoradial) and in type of ornament although the latter is variable within *Holmesocrinus*.

### **Shintocrinus cometensis** sp. nov.
(Figs 67, 68)

ETYMOLOGY. From the vicinity of Comet Creek Mine.

MATERIAL. HOLOTYPE: NMVP109778. PARATYPES: NMVP109771, 109801, 109803, 109808, 109812, 109818, 149366-149368 all from NMVPL300.

DIAGNOSIS. Cup low conical; thecal plates with many radiating rays (i.e. more than 1 per side) particularly in basal circlet; radials about as long as wide; radial facet very narrow, circular;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two anal plates in cup; radianal subquadrate, below and just left of C radial; anal X large with dominant radial ornament; anal sac longer than arms, with 4 strong vertical ridges joined by finer diagonal ridges, with distal portion of irregular polygonal plates; stem circular.

DESCRIPTION. Crown conical, 35mm long, with arms 6 times as long as cup. Cup low conical, slightly wider than long. Thecal plates thin, ornamented with broad low radial ridges continuing across sutures between basal and radial circlets and anal plates.

Infrabasals 5, pentagonal, about as wide as long, smallest plates of cup, upflared, completely visible in lateral view except for proximal flange resting on stem, smooth except for broad low ridge on distal sutural margins connecting to similar ridges on adjacent basals. Basals 5, hexagonal, about as wide as long, about same size as radials, with low wide main ridges forming vertically elongate cross and continuing to radials and infrabasals, with horizontal secondary ridges (2 or 4) continuing horizontally onto adjacent basals; posterior basal heptagonal, supporting anal X distally, with strong ridge from centre continuing onto anal X and distally along anal sac, with strong upper ridge running onto radianal rather than C radial. Radials 5, pentagonal, as wide as long, with 4 prominent ridges radiating from centre just proximal to radial facet and continuous onto adjacent basals, radials, anal X or radianal; radial facet angustary, U-shaped, with distal 1/2 of radial extending distally around facet. Anal plates in cup 2: anal X pentagonal, in radial circlet, with 5 strong radial ridges to posterior basal, anal sac, adjacent radials and radianal; radianal subquadrate, proximal and left of C radial, with broad low crossed ridges continuing to contiguous plates. Anal sac longer than arms, consisting of columns of plicate anals proximall y becoming less regular and polygonal distally, with strong low wide ridge along posterior side on proximal portion. Arms isotomous, narrow, deep U-shaped sectional shape, with angular outer edge, dividing 4 times at 4th primibrach, 4th secundibrach, 7th tertibrach and at a similar distance again (no specimen well enough preserved to be able to count distal brachials). Stem circular in section, of uniform diameter over available length, irregularly dimorphic with some sections of stem having 3 or 4 identical columnals adjacent to each other but most of stem with nodals of larger diameter alternating with smaller internodals in noditaxis pattern N212, with subtle expression of decagonal section in some internodals in some specimens.

REMARKS. This species is distinguished from *S. richi* by its cup plate ornament with secondary ridges, probably by the shape of the radianal and by the slightly different stem structure. The Swedish *S. costatus* has some secondary ridges on the thecal plates but the major ridges are still narrow and discrete by comparison with the Australian species.

**Shintocrinus richi** sp. nov.
(Figs 65A, 66A)

ETYMOLOGY. For Tom Rich, my former colleague at the Museum of Victoria.

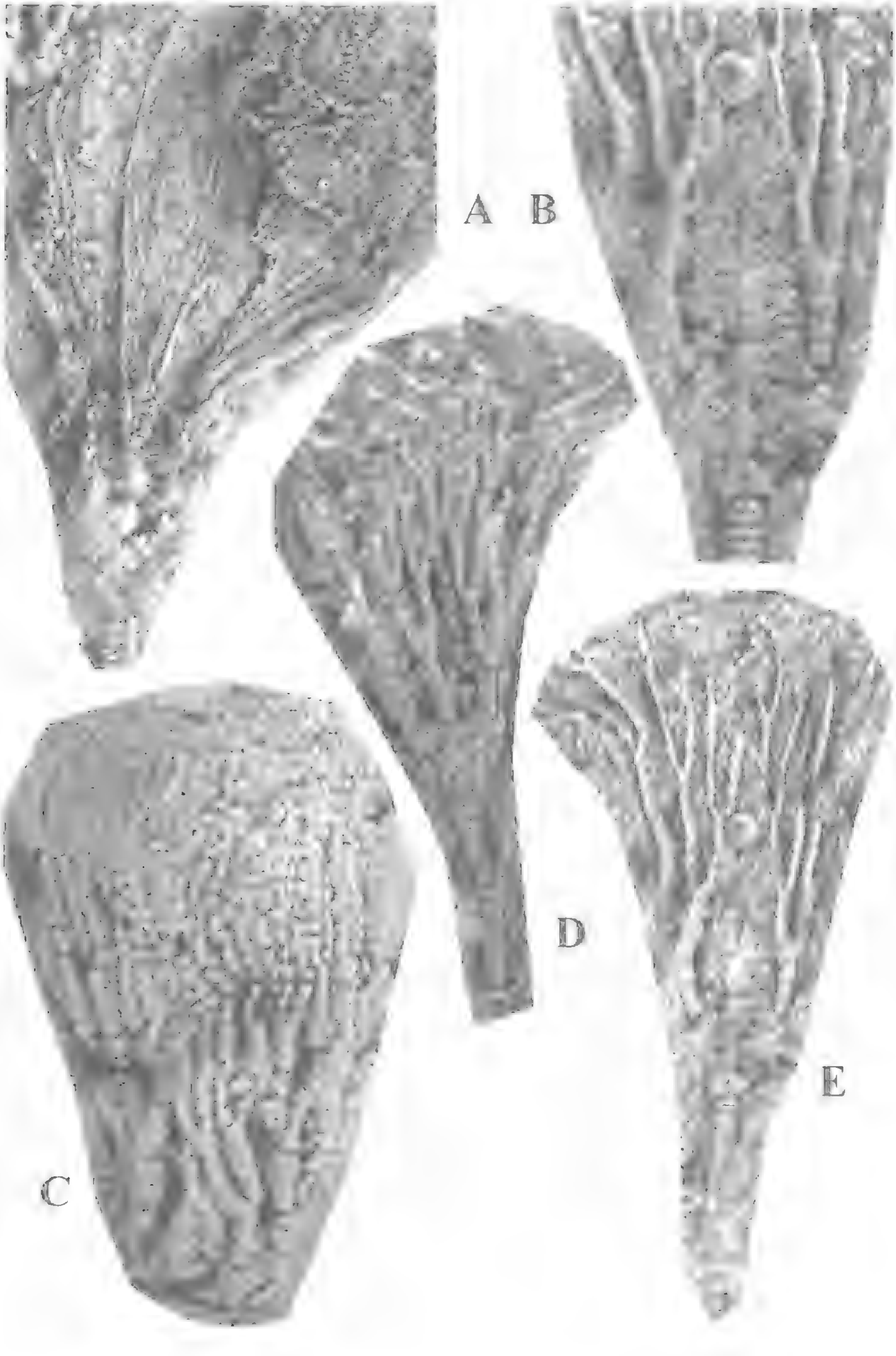
MATERIAL. HOLOTYPE: NMVP149390 from NMVPL1990.

DIAGNOSIS. Radianal large, pentagonal, proximal and left of C radial. Thecal plate ornament of fine radial ridges continuing distally on anal tube.

DESCRIPTION. Crown conical, estimated 50mm long. Cup low conical. Thecal plates thin, ornamented with narrow wire-like radial ridges continuing across sutures between all cup and anal tube plates.

Infrabasals and basals collapsed, indistinct except for part of BC basal showing ornament. Radials 5, pentagonal, as wide as long, with 4 prominent ridges radiating from centre just proximal to radial facet and continuous onto adjacent basals, radials, anal X or radianal; radial facet angustary, U-shaped, with distal 1/2 of radial extending distally around facet. Anal plates in cup 2: anal X 7-sided, in radial circlet, large with 7 radial ridges to posterior basal, anal sac, adjacent radials and radianal, with vertical ones stronger than others; radianal proximal and left of C radial, with 5 fine radial ridges suggesting pentagonal shape (outline not clear). Anal sac long, of columns of plicate anals, with strong ridge along posterior side proximally. Arms isotomous, narrow, deep U-shaped sectional shape, with angular outer edge, dividing at least 3

FIG. 67. *Shintocrinus cometensis* sp. nov., all crowns from NMVPL300. A, NMVP149366, ×3. B, NMVP109818, ×3. C,F, D ray view of NMVP109801, ×3 and ×6. D, C ray view of NMVP149367, ×3. E, NMVP109803, ×3. G, NMVP109812, ×2.75.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(and probably 4) times, first division at 4th primibrach. Stem circular in section, of uniform diameter over available length, heteromorphic, columnals long, of uniform diameter, with latus near midlength of differing widths.

REMARKS. This species is based on a single crushed and poorly preserved specimen preserved in friable siltstone so its assignment could be considered tentative. It is distinguished from other species of the genus by its sharp fine radial ridge ornament and probably pentagonal radianal. Its crown resembles that of *Plicodendrocrinus australis* sp. nov. but that species has its radianal directly beneath the C radial and a distinctive stem although the proximal part of its stem resembles that of *S. richi*. Doubtless these species of *Plicodendrocrinus* and *Shintocrinus* are closely related but knowledge of the Australian species is poor so I refrain from any speculation on relationships.

### **Holmesocrinus** gen. nov.

TYPE SPECIES. *Holmesocrinus enidae* sp. nov.

ETYMOLOGY. For Frank and Enid Holmes of Melbourne for their unstinting assistance in the field and donation of specimens. The specific epithet is for Enid who collected the holotype.

DIAGNOSIS. Cup long, slender, conical. Thecal plates with prominent radial ridge ornament or smooth. Infrabasals 5, pentagonal, with ridges crossing close to proximal margin and running into different lobes of stem. Basals 5, hexagonal except for heptagonal CD basal, with radial ridge ornament. Radials 5, with horseshoe-shaped facets more than 1/2 radial width; C radial with only 5 radiating ridges, smaller and further distally in cup than others. Arms uniserial, narrowly horseshoe-shaped in section, branching isotomously 4 times; primibrachs, secundibrachs and tertibrachs 4 or 5 axillary. Radianal pentagonal, proximal and slightly left of C radial; anal X heptagonal, in radial circlet, with 5 radiating ridges, supporting single anal plate above; anal tube as long as arms, of plicate plates. Stem pentalobate, heteromorphic, with large circular nodals separated by 3 pentagonal internodals the middle one being slightly wider than the other 2, noditaxis N212.

REMARKS. The prominent radial ridge ornament is distinctive of earliest cladids. *Aethocrinus* Ubaghs, 1969 (type species *A. moorei* Ubaghs, 1969 from the Lower Ordovician of southern France) is distinguished by the extra circlet of plates in the cup, pentameric stem and wider radial facet. *Holmesocrinus* is assigned to the Plicodendrocrinidae because of the width and horseshoe-shape of radial facets, long anal tube of plicate plates, uniserial non-pinnulate arms, 2 circlets of plates proximal to the radials and radianal situated proximal and only slightly left of the C radial. It differs from other members of the family principally in its distinctive stem structure of pentagonal internodals between greatly expanded circular nodals. It is further separated from *Plicodendrocrinus* by its radianal being proximal and left of the C radial and from *Compagicrinus* by having 1 radianal. It most closely resembles *Shintocrinus* but that genus has anal X in the radial circlet with its distal margin at the same level as the distal margin of the radials and a more elaborately ornamented and longer anal tube. *Shintocrinus* and *Holmesocrinus* almost certainly evolved from a common ancestor among Ordovician or Llandovery plicodendrocrinids but represent separate lineages clearly defined by the different stem structures.

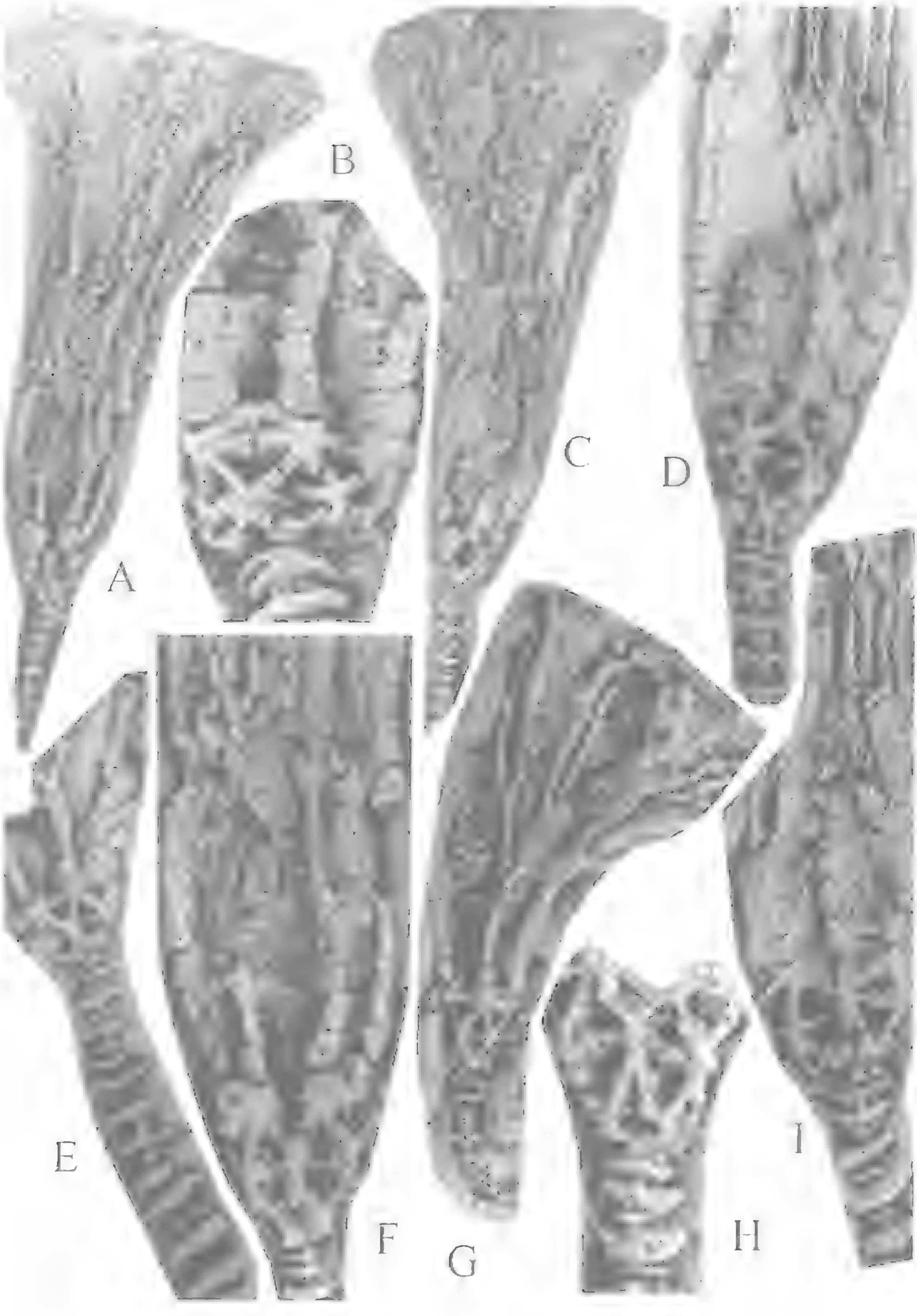
### **Holmesocrinus enidae** sp. nov.
(Figs 69, 70)

MATERIAL. HOLOTYPE: NMVP100112. PARATYPES: NMVP100102, 100104, 100107, 100108, 107107 all from NMVPL1923.

DIAGNOSIS. Cup strongly ornamented with prominent narrow radial ridges on all plates. Radianal with 5 radiating ridges.

DESCRIPTION. Crown subcylindrical, 45mm long, with arms more than 8 times as long as cup. Cup low conical. Infrabasals 5, each with midline running into a longitudinal groove on stem, with rounded ridges emanating from near bottom corners then crossing near proximal edge and extending across distal sutures at right angles, without transverse circular ridge. Basals 5, hexagonal, each with 3 ridges normal to margins and crossing each other in middle of plate, with ridges continuous with others on adjacent circlets and third with annular ridge on other basals; CD basal heptagonal, with extra ridge beginning at

FIG. 68. *Shintocrinus cometensis* sp. nov., all crowns in lateral view from NMVPL300. A, posterior view of NMVP109771, ×2.75. B,E, posterior view of holotype NMVP109778, ×6 and ×3, respectively. C, posterior view of NMVP109808, ×4. D, NMVP149368, ×3.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midpoint and running distally across anal X onto anal tube, otherwise ridges same as on basals. Radials in contact except in posterior interray where anal X intervenes in circlet, hexagonal, with horseshoe-shaped radial facet almost horizontal to slightly downsloping and occupying approximately 1/2 width of plate, with same 3 ridges as on basals but crossing just proximal to radial facet, with separate ridge beginning at point of crossing of other 3 and running distally along arm, with 2 diagonal ridges finishing at distal margin of radial; C radial smaller than others, further distally in cup than others, with B radial proximal and right of it so that 1 ridge does not continue and only 5 plus the arm meet in the crossing of the ridges, in contact with radianal and anal X radianal pentagonal, with some variation in ridge pattern across it but with ridges crossing each suture at right angles to continue 2 diagonal ridges but introducing a section of transverse ridge that is between the basal and radial circular ridges; anal X 7-sided, supporting very long anal tube of strongly plicate plates. Arms narrowly horseshoe-shaped in section, with primibrach 4 or 5 axillary with apparent consistency in each individual, with brachials becoming shorter distally, with 1st secundibrachs and 1st tertibrachs in contact for a short distance (< height of the columnal) distal to the midline of the axillary. Stem pentagonal to pentalobate in section, becoming circular distally, heteromorphic; nodals large, circular, twice diameter of rest of stem, almost twice length of other columnals; noditaxis N212; full length of stem not known.

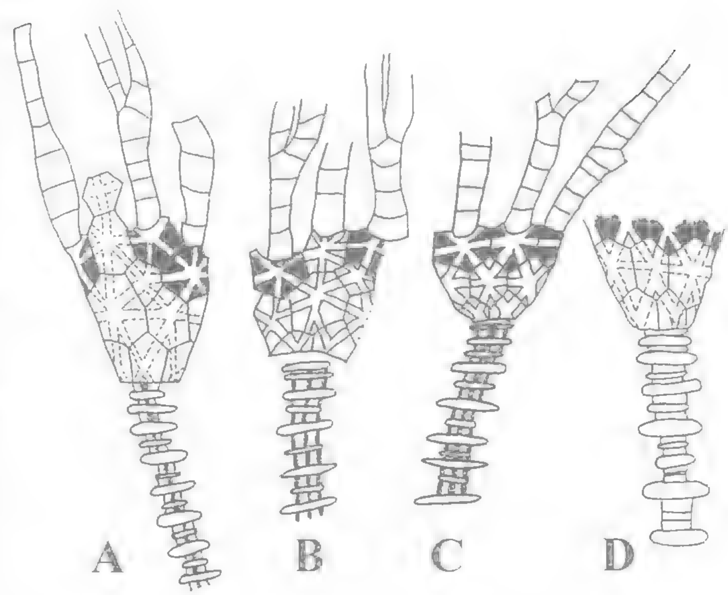



FIG. 70. *Holmesocrinus enidae* gen. et sp. nov., sketches of plate arrangements with radial ridge ornament shown on cup plates and radials black except for the radial ridges. A,B, NMVP100112 (Fig. 69C) and NMVP100102 (Fig. 69I), respectively, in posterior view showing pentagonal radianal. C, D, NMVP100107 (Fig. 69E) and NMVP100108 (Fig. 69H), respectively, in anterior view.

REMARKS. There is some variation in cup shape with those that are more narrowly conical also having almost knife-edged outer faces to arms. This suggests that there has been some degree of tectonic compression of those specimens but such distortion is not uniform in the echinoderms or the co-occurring brachiopods. There has been a certain amount of dislocation of cup plates in some specimens and the sutures are not clear on several specimens as they are deep in the recesses between ridges. Nevertheless sutures are readily determined by projecting the suture from where it crosses the ridge. There is some intraspecific variation in which brachials are axillary and also in the structure of the stem (order of columnals) but in general it is a uniform species. It is distinguished from all other plicodendrocrinids by the nature of its stem except for *H. idaensis* which has an unornamented cup.

**Holmeseocrinus idaensis** sp. nov.
(Fig. 71)

ETYMOLOGY. For Mount Ida, north of Heathcote, in the vicinity where the species occurs.

MATERIAL. HOLOTYPE: NMVP59256 (counterpart – NMVP148625). PARATYPE: 148623 from locality 52 of Thomas (see Talent, 1965, fig. 1), Parish of Redcastle, N of Heathcote, in clean orthoquartzite.

FIG. 69. *Holmesocrinus enidae* gen. et sp. nov., all crowns from NMVPL1923. A,F, C,D, part and counterpart of holotype NMVP100112, ×2, ×4, ×2 and ×4, respectively. B, NMVP100104, ×5. E, NMVP100107, ×2.5. G, NMVP107107, ×3. H, NMVP100108, ×5. I, NMVP100102, ×3.5.

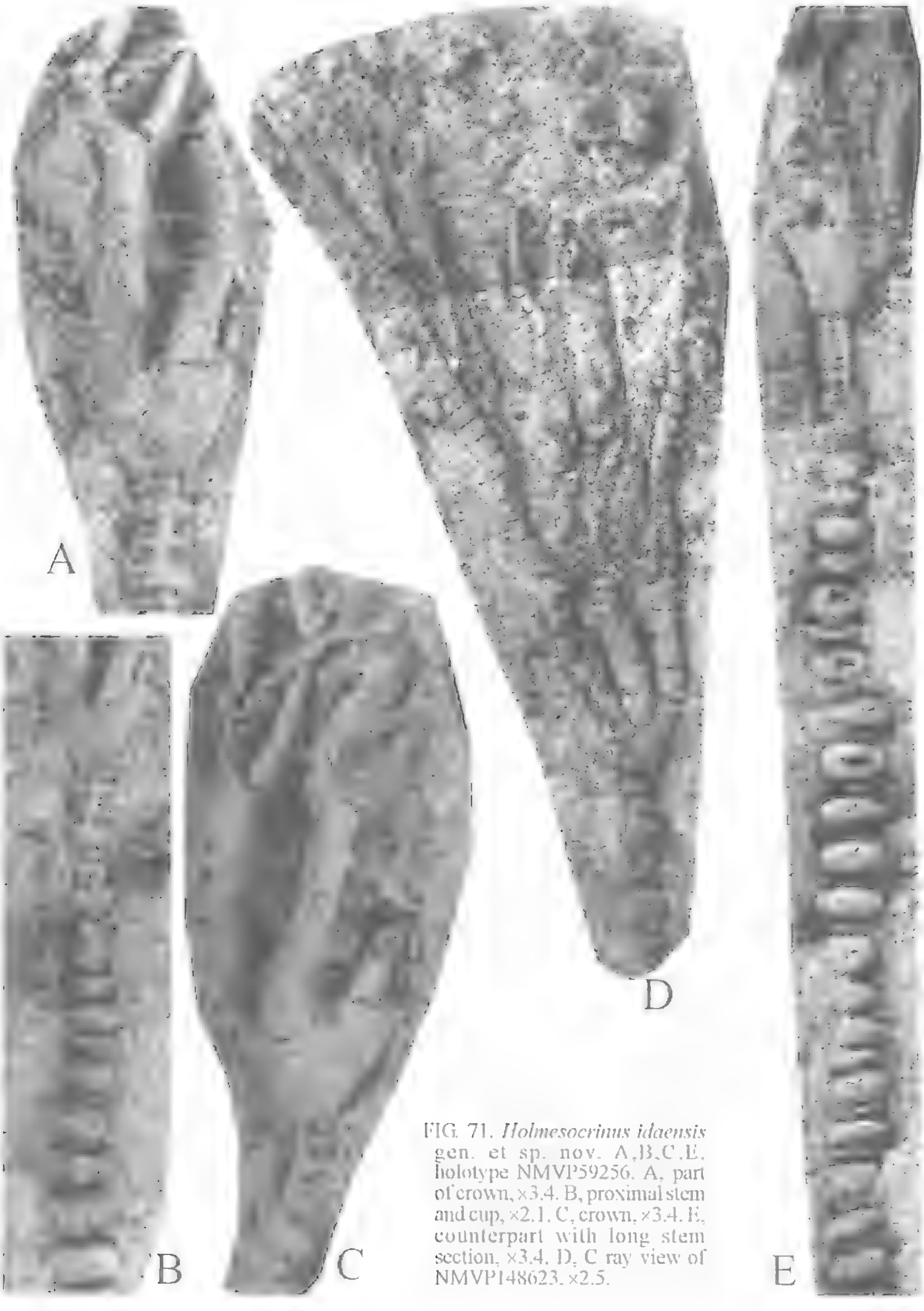



FIG. 71. *Holmesocrinus idaensis* gen. et sp. nov. A,B,C,E, holotype NMVP59256. A, part of crown, ×3.4. B, proximal stem and cup, ×2.1. C, crown, ×3.4. E, counterpart with long stem section, ×3.4. D, C ray view of NMVP148623, ×2.5.

DIAGNOSIS. Crown conical, 45mm long. Cup smooth, without radiating ridges. Stem with nodals barely wider than internodals proximally, becoming greatly enlarged distally with rounded latus.

DESCRIPTION. Cup low conical, as long as wide. Thecal plates thick, smooth, slightly depressed at corners. Infrabasals 5, pentagonal, as long as wide, upflared, fully visible laterally except for lower flange resting on stem, with central basal projection in line with angle of stem. Basals 5, about as long as wide; posterior basal 7-sided, supporting the anal X distally across a horizontal suture. Radials 5, pentagonal, as long as wide, largest plates in cup; radial facet, peneplenary to plenary, round, subhorizontal. Two anal plates in cup: radianal quadrate to rectangular, proximal and left of C radial; anal X in radial circlet, same shape as radials. Anal sac poorly preserved, with central posterior column of smooth plates, may be short slim and straight, mostly unknown. Arms isotomous, narrow, deep U-shaped cross section, dividing 3 times on 4th-6th brachial each time; brachials rectangular, nonpinnulate. Stem pentagonal in section proximally, heteromorphic, noditaxis N1, with nodals up to and sometimes more than twice as long as and slightly wider than internodals; distally internodals becoming exceptionally expanded, with rounded latus.

REMARKS. Generic assignment of this taxon depends heavily on stem structure which matches that of *H. enidae* very closely in having pentagonal internodals and greatly expanded circular nodals with priminternodals becoming circular distally. The difference in cup ornament could be considered a generic feature but this disparity is observed between congeneric species in other dendrocrinoid genera and so *Holmesocrinus* is considered best identified by the stem structure. As in *H. enidae* the radianal is proximal and left of the C radial, the radial facets are peneplenary and the arms branch isotomously.

## Family THALAMOCRINIDAE Miller & Gurley, 1895

The family was broadly interpreted by McIntosh (1979) to include 13 genera but he (1983) later redefined the family more closely with 7 genera including 3 genera not included in 1979. In 1988 McIntosh & Brett recognised the priority of Thalamocrinidae and reorganised the family content once more. We acknowledge that classification of primitive cladids is far from settled at both familial and generic levels and thus retain the broader concept of the family.

### **Antihomocrinus** Schmidt, 1934

TYPE SPECIES. *Homocrinus tenuis* Bather, 1893 from the Wenlock of Gotland, Sweden.

DIAGNOSIS. Cup high conical; thecal plates smooth, thick; 2 anal plates in cup; radianal quadrangular; anal sac straight, long, nonplicate; radial facets peneplenary; arms branching isotomously on first 2 divisions, third divisions may be at different heights in same ray; stem circular in section, heteromorphic proximally.

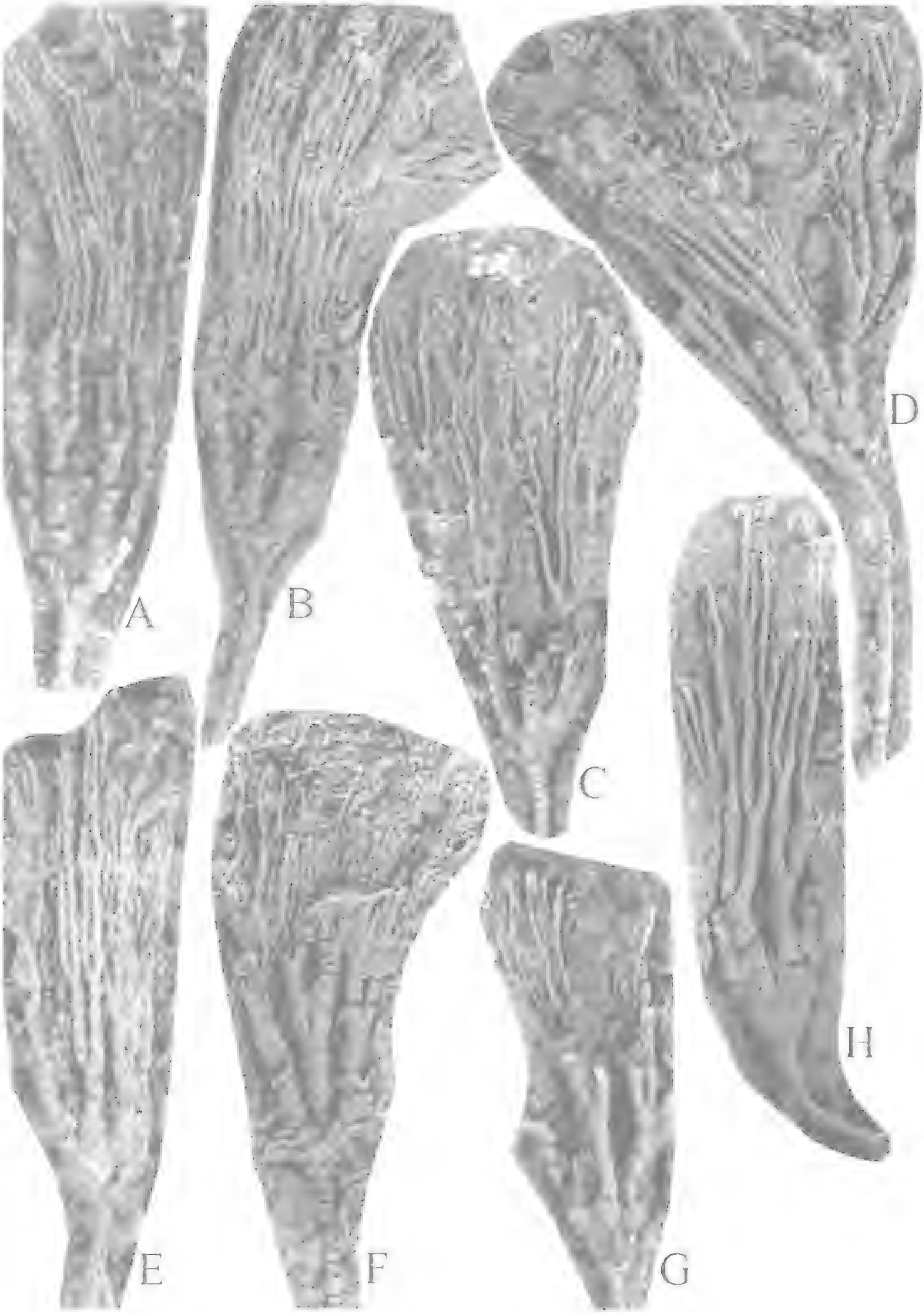
REMARKS. The type species has a round stem whereas other species assigned by Schmidt (1934, 1941) have pentagonal stems and may not belong to the same lineage. There is little to choose between *Bactrocrinites* and *Antihomocrinus* and indeed Schmidt's (1934) original diagnosis mentioned only that the infrabasals and basals of *Antihomocrinus* were more normally proportioned i.e. not elongate as in *Bactrocrinites*. The Australian species is assigned here on the basis that its cup plates are not nearly as elongate as in *Bactrocrinites* and its stem is round in section as opposed to pentagonal in *Bactrocrinites* (Schultze, 1867, pl. 5, fig. 1g).

McIntosh (1983) noted the only significant distinction between the type species of *Antihomocrinus* and *Lasiocrinus* Kirk, 1914 as the isotomous vs. heterotomous arm branching, respectively. The new Australian species has isotomous arm branching in the lower 2 divisions but the 3rd divisions, in many cases, are at different heights in the same arm. In at least one specimen (Fig. 75A-C) the arms branch isotomously but the branches nearest to the central axis of the ray form 2 straight vertical columns and all lateral branches move asymmetrically away from the central axis. These features could be regarded as beginning to evolve from isotomous towards heterotomous arms and thus intermediate between the 2 genera. I place the new species in *Antihomocrinus* because the arm branching comes closer to the isotomous condition.

### **Antihomocrinus chapmani** sp. nov.
(Figs 72-77)

ETYMOLOGY. For Frederick Chapman, for his contribution to Victorian Palaeozoic faunal studies.

MATERIAL. HOLOTYPE: NMVP108630. PARATYPES: NMVP100170, 108606, 108612, 108616, 108631, 108632, 108639, 108648, 108687, 109769,


A
B
C
D
E
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H

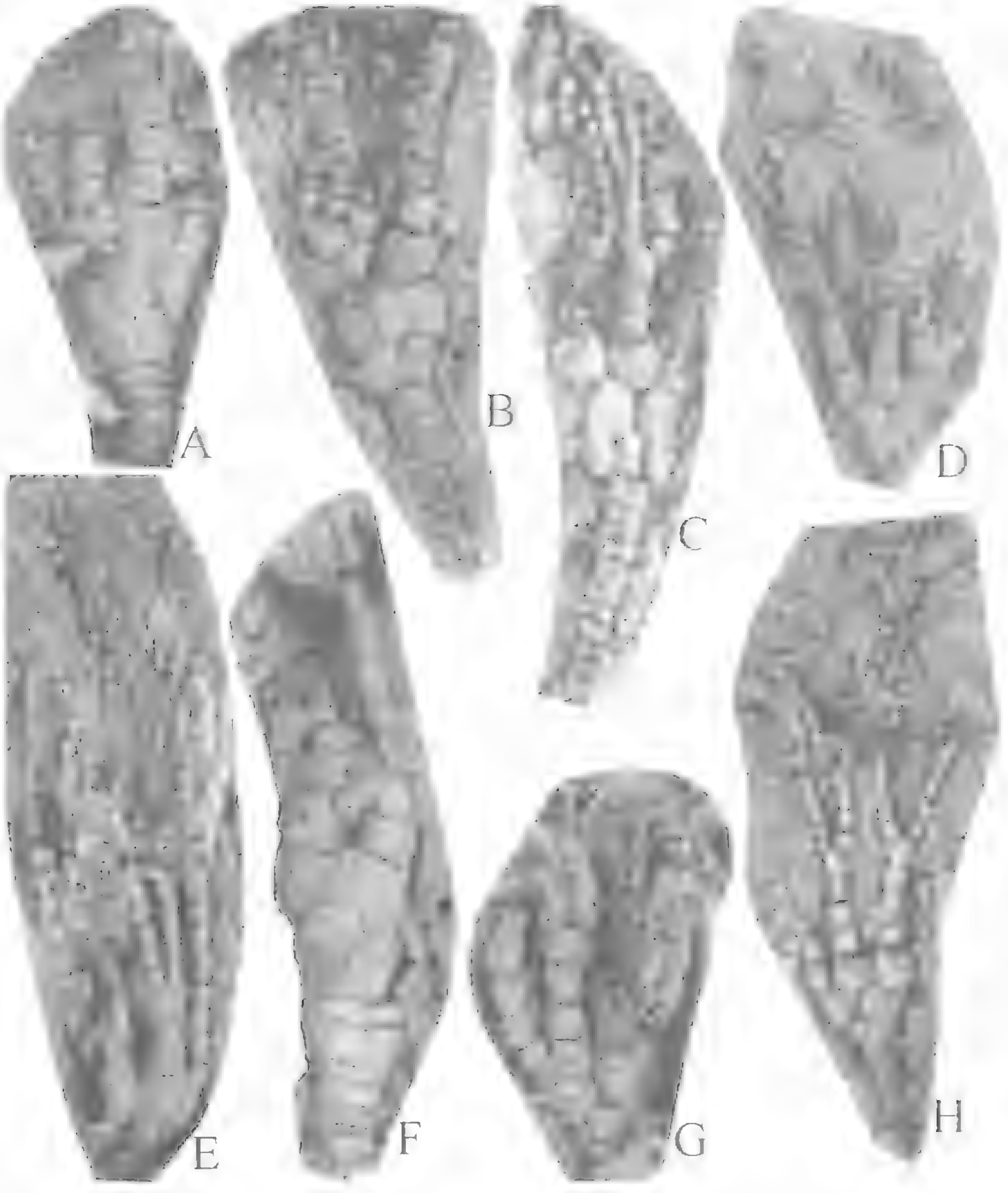


FIG. 73. *Antihomocrinus chapmani* sp. nov., all incomplete crowns from NMVPL1924. A,F, part and counterpart of NMVP109757, ×3 (F with radianal central). B,C, part and counterpart of NMVP109225, ×3. D,H, part and counterpart of NMVP109217, ×3. E, NMVP109227, ×3. G, NMVP109751, ×3.

FIG. 72. *Antihomocrinus chapmani* sp. nov., all crowns in lateral view from NMVPL300. A, NMVP149369 ×2.7. B, NMVP109797, ×2.7. C, NMVP109792, ×2.7. D, C ray view of NMVP109770, ×2.7. E, NMVP110625, ×2.7. F, NMVP149370, ×2.7. G, NMVP149371, ×2.7. H, NMVP109799, ×2.7.

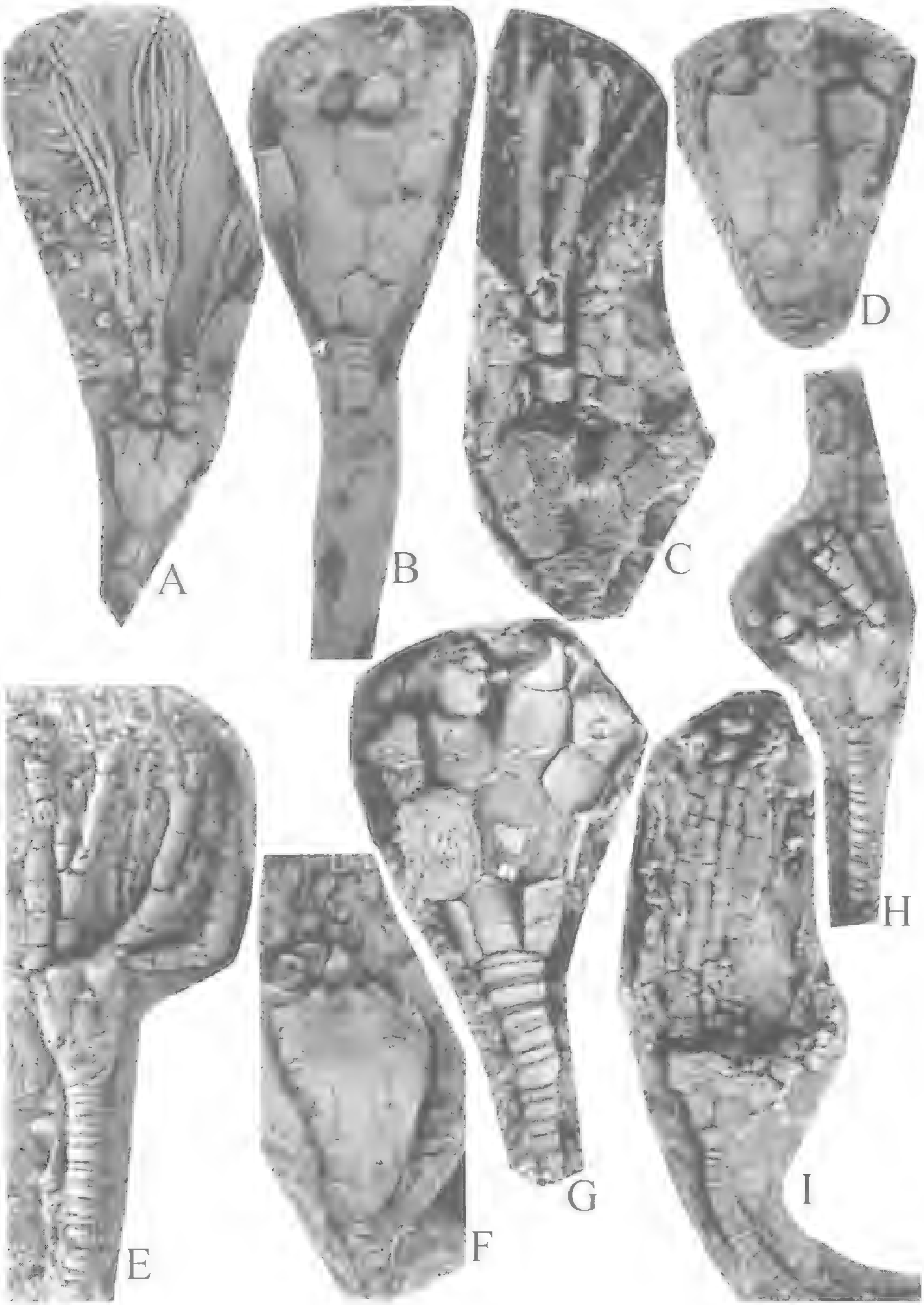


FIG. 74. *Antihomocrinus chapmani* sp. nov., all lateral views of incomplete crowns from NMVPL252 except F from Chirnside Park (NMVPL1922). A, anterior view of crown NMVP109769, ×2.4. B,D, part and counterpart of cup NMVP108616, ×2.4. C, posterior view including part of anal tube of NMVP149360, ×2.4. E, anterior view of crown with anal tube evident NMVP149372, ×2.4. F, cup NMVP107090, ×2.4. G, D ray view of cup NMVP108687, ×2.4. I, anterior view of crown with anal tube but no arms preserved NMVP149361, ×3.2. H, *Dictenocrinus ibaeypus* sp. nov., anterior view of crown NMVP108612, ×2.5.

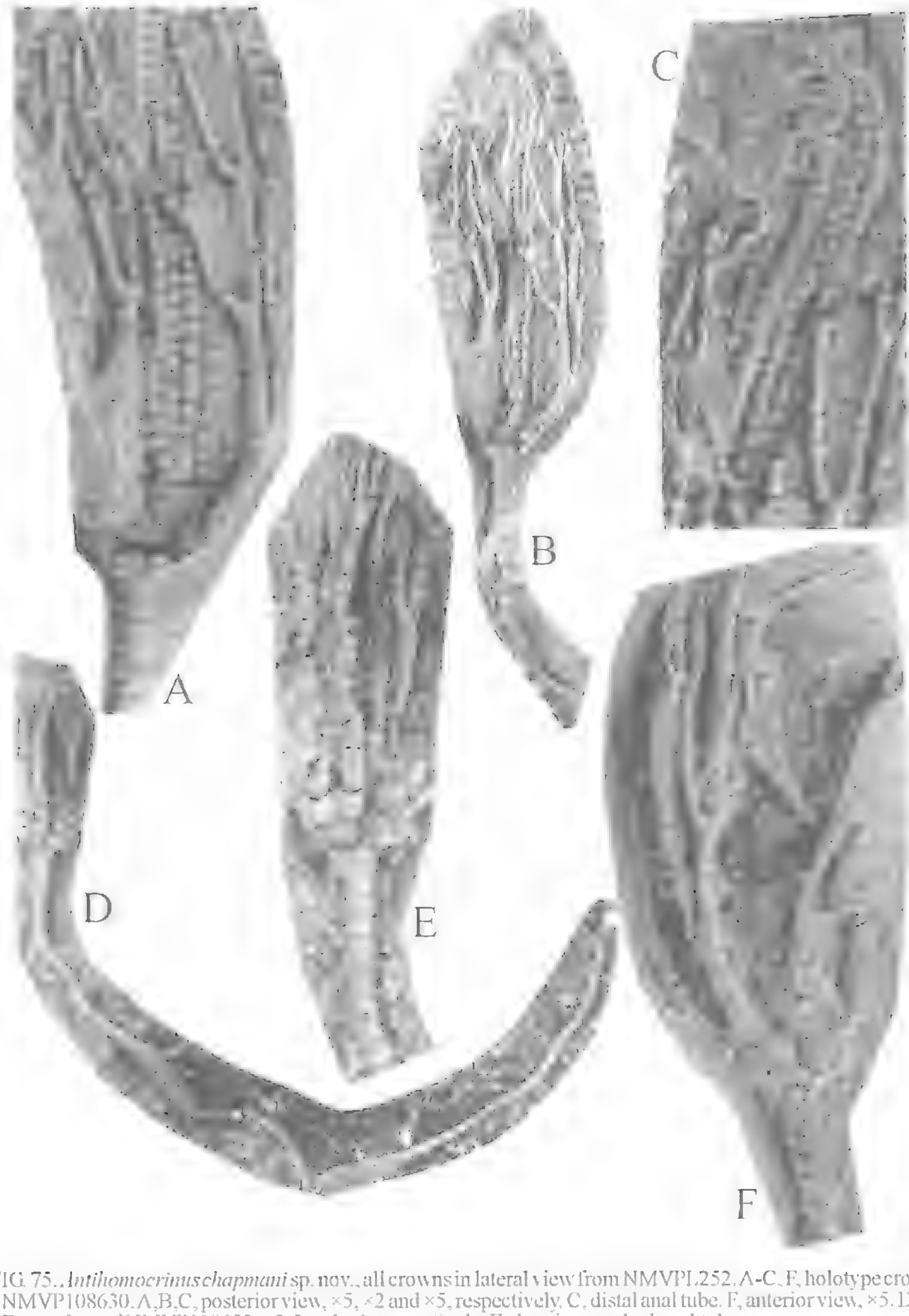


FIG. 75. *Intihomocrinus chapmani* sp. nov., all crowns in lateral view from NMVPL252. A-C, F, holotype crown NMVP108630. A, B, C, posterior view, ×5, ×2 and ×5, respectively. C, distal anal tube. F, anterior view, ×5. D, E, D ray view of NMVP108632, ×2.5 and ×4, respectively. E showing crushed anal tube.

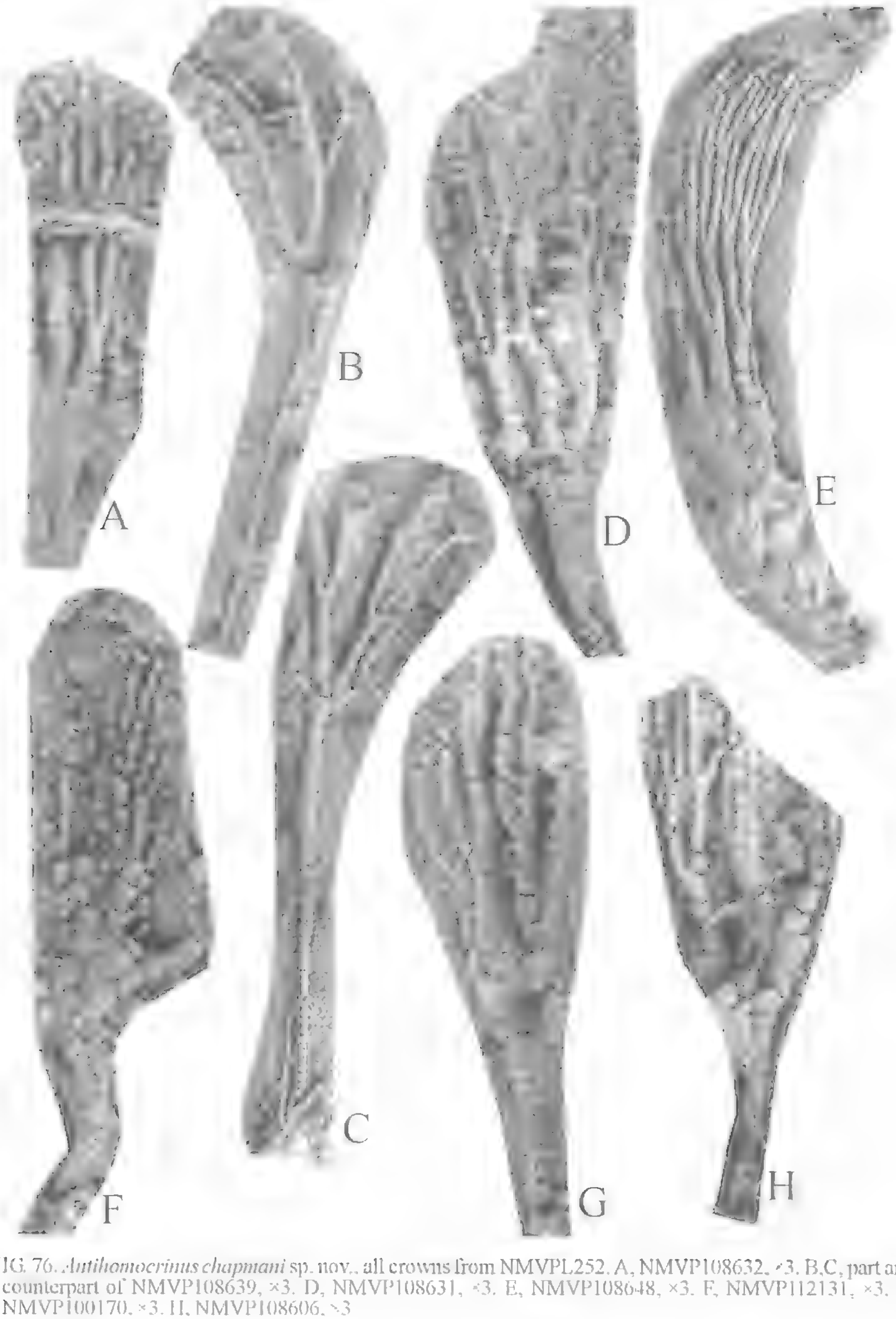


FIG. 76. *Antihomocrinus chapmani* sp. nov., all crowns from NMVPL252. A, NMVP108632, ×3. B,C, part and counterpart of NMVP108639, ×3. D, NMVP108631, ×3. E, NMVP108648, ×3. F, NMVP112131, ×3. G, NMVP100170, ×3. H, NMVP108606, ×3

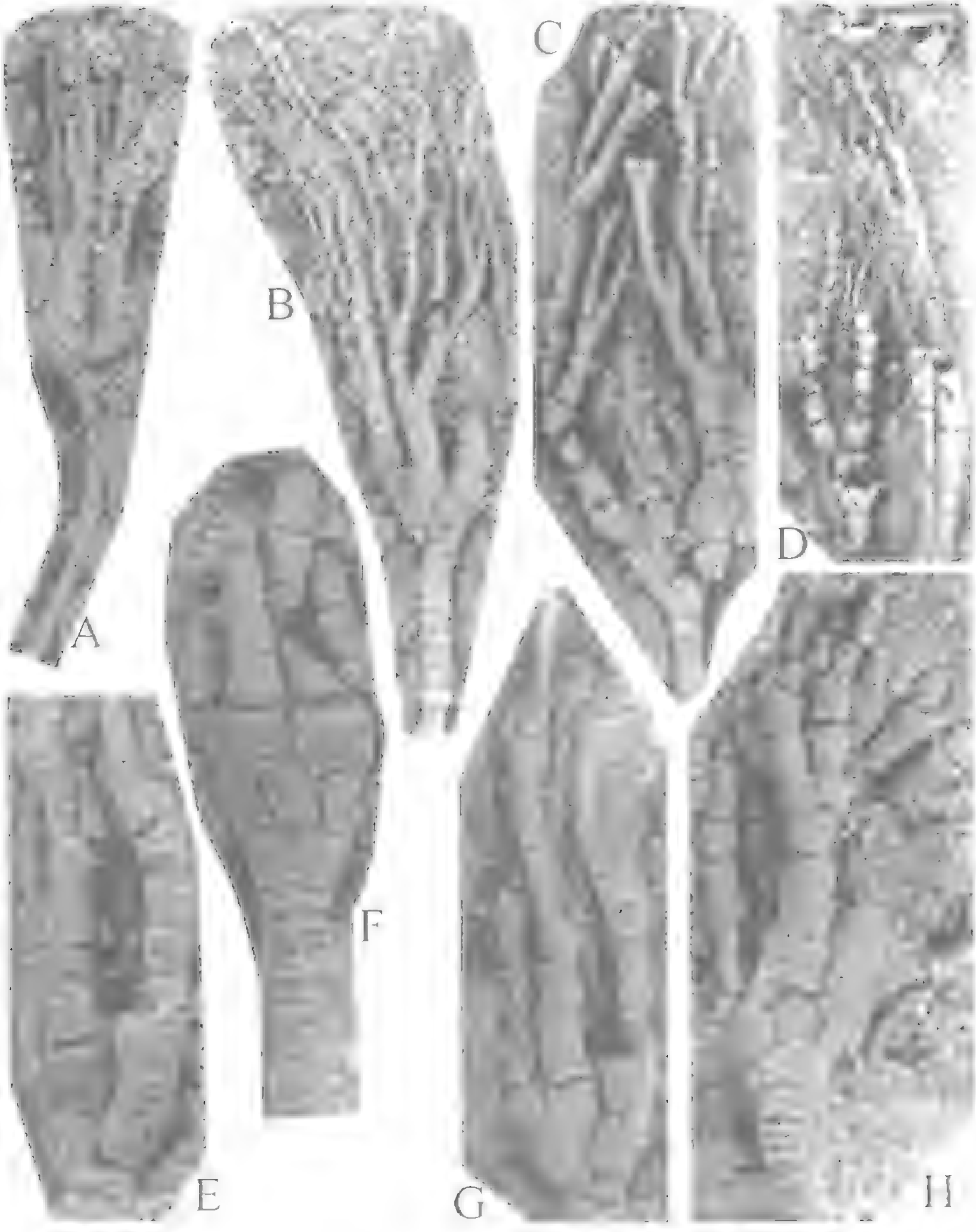


FIG. 77. *Antihomocrinus chapmani* sp. nov., all crowns or partial crowns from NMVPL229. A, NMVP108688, ×3. B, NMVP109157, ×3. C,D, part and counterpart of NMVP100167, ×3 and ×2, respectively. E-G NMVP100154, ×5, ×5 and ×3, respectively. H, NMVP108953, ×3.

112131, 149360, 149361, 149372 from NMVPL252. NMVP109217, 109225, 109227, 109751, 109757 from NMVPL1924; NMVP107090 from Chirnside Park Estate, Lilydale. NMVP100154, 100167, 108688, 108953, 109157 from NMVPL229; NMVP109770, 109792, 109797, 109799, 110625, 149369-149271 from NMVPL300.

DIAGNOSIS. Cup high conical. Infrabasals almost as long as basals. Radial facets angustary. Arms uniserial, branching isotomously up to 4 times. Anal tube long, with curved tip, of vertical columns of smooth (smaller specimens) to radially ornamented polygonal plates. Stem circular in section, heteromorphic, becoming uniform distally; nodals longer but only slightly wider than alternating internodals.

DESCRIPTION. Crown 30mm long, subcylindrical to subconical with distal arms flaring slightly. Cup conical, longer than wide. Thecal plates thick, smooth. Infrabasals 5, pentagonal, from 0.5 up to twice as long as wide, upflared, fully visible laterally except for lower flange resting on stem. Basals 5, same size or larger than radials, longer than wide; posterior basal 7-sided, supporting the radianal distally and slightly to the right across an oblique suture, with distal sutural margin supporting anal X not quite horizontal. Radials 5, pentagonal, as long as wide; radial facet, peneplenary, round, subhorizontal, not declined. Anal plates in cup 3; radianal quadrate, proximal and left of C radial; anal X in radial circlet, same shape as but slightly smaller (i.e. not extending as far distally) than radials; proximal part of 3rd anal plate below distal margin of C radial. Anal sac long, of vertical columns of small smooth hexagonal plates, with plates in alternate columns bearing stellate ornament in larger individualals (merely depressed corners in smaller individuals), with curved tip. Arms isotomous, almost circular in cross section, dividing 3 or 4 times on 3rd-5th primibrach, 3rd or 5th secundibrach and on 7th tertibrach, uniserial with rectangular brachials throughout, with deep V-shaped furrow on inner side, nonpinnulate, with 1st and 2nd divisions always at same level but with other divisions sometimes at different levels in same arm. Stem circular in section, noditaxis N1, with nodals up to and sometimes more than twice as long as and slightly wider than internodals, with fine central canal.

REMARKS. I initially separated this material into 3 species based on relative sizes of infrabasals to basals, numbers of primibrachs per arm, width of the radial facet and relative sizes of the radianal. Although there is some consistency of the variation in these features between localities there are numerous exceptions and I think it more likely the collections from different localities represent variable populations (the variants in different proportions) of a long ranging (Ludlow to Lochkovian) species. A large number of illustrations are provided to show the variation as much as possible.

It differs from the German species in its round rather than pentagonal stem and from the type species by the stellate ornament on anal tube and heteromorphic stem but it is close to the type.

### **Ancyrocrinus** Hall, 1862

TYPE SPECIES. *Ancyrocrinus bulbosus* Hall, 1862 from the Middle Devonian of New York.

### **Ancyrocrinus** sp. (Fig. 78)

MATERIAL. NMVP107105 from NMVPL229.

DESCRIPTION. Cup cylindrical, as long as wide. Thecal plates smooth. Infrabasals 5, pentagonal, wider than long, upflared, fully visible laterally except for lower flange resting on stem. Basals 5, largest plates in cup, only slightly longer than wide; posterior basal 7-sided, supporting the anal X distally across a horizontal suture. Radials 5, pentagonal, as long as wide; radial facet peneplenary, round, declivate. Two anal plates in cup: radianal quadrate, proximal and left of C radial; anal X in radial circlet, similar size and shape to radials. Anal sac tall, of smooth polygonal plates. Arms almost circular in cross section, with deep U-shaped furrow on inner side, with 3rd primibrach axillary, uniserial with rectangular brachials throughout. Stem rounded subquadrate or subpentagonal in section, heteromorphic, with nodals much longer and slightly wider than internodals.

REMARKS. This incomplete specimen is assigned to *Ancyrocrinus* based on cup shape, shape position and size of radianal and shape of the stem. The most distinctive feature of the genus, the grapnelhook termination to the stem has not been found at this locality but other features are sufficient for assignment. It is left in open nomenclature because it is incomplete and a single specimen.

### **Nassoviocrinus** Jaekel, 1918

TYPE SPECIES. *Heterocrinus pachydactylus* Sandberger & Sandberger, 1855 from the Lower Devonian of Germany.


FIG. 78. *Ancyrocrinus* sp. A, crown with incomplete arms NMVP107105 from NMVPL229, ×4. B, sketch showing posterior plate arragement (C radial heavily outlined).

DIAGNOSIS. Cup low conical; thecal plates with or without ornament; radianal quadrangular; radial facets angustary to peneplenary; anal sac long, straight, of regular columns of small plicate plates; arms isotomous, branching 3 or more times; stem pentagonal, heteromorphic.

REMARKS. McIntosh (1983) reviewed this genus assigning 6 species from the Lower and Middle Devonian of Europe and North America. These Australian Ludlow species are assigned by comparison with the type species with which they share the pentagonal heteromorphic stem, quadrangular radianal, isotomous arms and general shape and proportions of the cup. Although *N. longibrachiatus* has perfectly smooth thecal plates unlike European representatives, the depressed corners of thecal plates in *N. corcorani* are comparable with other members of the genus.

**Nassoviocrinus longibrachiatus**
(Chapman, 1903) (Fig. 79)

*Botryocrinus longibrachiatus* Chapman, 1903:108, pl. 18, figs 6-8.

MATERIAL. LECTOTYPE: (designated here) NMVP390 & 392 (part and counterpart) from NMVPL1615. Other material NMVP109174, 109176 from NMVPL1615 and NMVP109177-109179 from the Upper Yarra.

DIAGNOSIS. Cup low conical; thecal plates smooth, unornamented; radial facet peneplenary; radianal quadrangular; anal X supporting 3 anal plates distally; anal tube long, straight, of vertical columns of plicate plates; arms branching isotomously, at least 3 times; stem pentastellate in section, heteromorphic.

DESCRIPTION. Crown subcylindrical, 35mm long. Cup low conical, wider than long. Thecal plates smooth, without ridges. Infrabasals 5, pentagonal, wider than long, with lateral basal corners projecting slightly where they extend onto the projections in the stem. Basals 5, hexagonal, longer than wide, largest plates in cup; posterior basal with 7th side on distal margin, supporting anal X distally. Radials 5, pentagonal, wider than long; radial facet angustary to peneplenary, subcircular, with deep ventral groove. Anal plates in cup 2; radianal quadrangular, proximal and left of C radial, with diagonals horizontal and vertical; anal X heptagonal, wider than long, in radial circlet, supporting 3 plates at base of anal sac. Anal sac long, narrow, straight, of plates with radial ridges (2 in each direction laterally and 1 each distoproximally) arranged in vertical columns, with larger proximal central plate having ridges only near upper margin, with lateral basal plates much smaller than central one. Arms isotomous, branching at least 3 times, deep U-shaped in section (i.e. laterally compressed), with deep groove on inner side; primibrach 4 axillary except in A ray where 5th primibrach is axillary; axillary secundibrach variable 6-8. Stem pentastellate, heteromorphic, noditaxis N212.

REMARKS. This species is assigned to *Nassoviocrinus* on the basis of its quadrangular radianal.

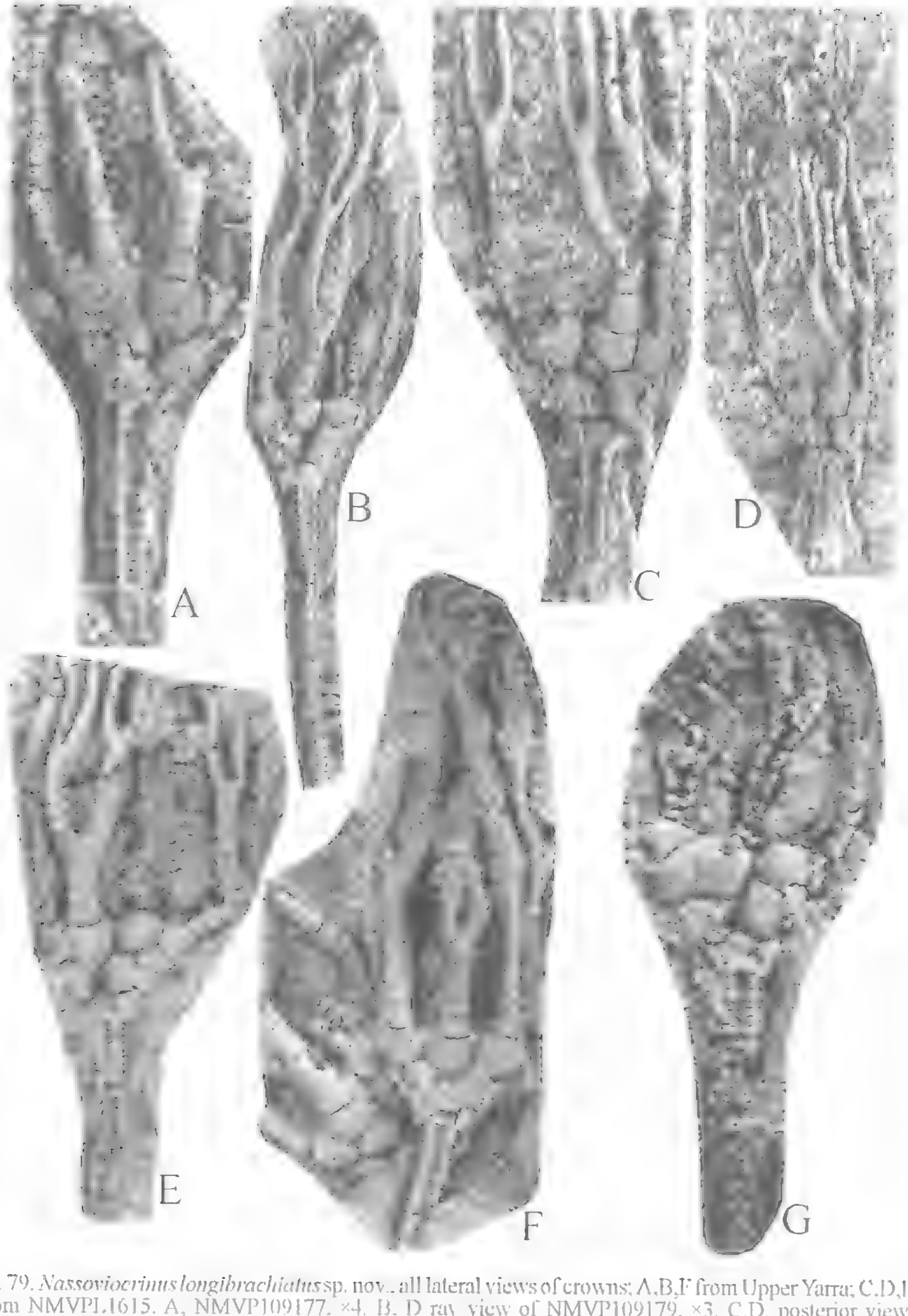


FIG. 79. *Nassoviocrinus longibrachiatus* sp. nov., all lateral views of crowns; A,B,F from Upper Yarra; C,D,E,G from NMVPL1615. A, NMVP109177, ×4. B, D ray view of NMVP109179, ×3. C,D, posterior view of NMVP109176, ×4 and ×2.5, respectively. E, posterior view of NMVP109174, ×4. F, two crowns overlying each other NMVP109178, ×2.5. G, posterior view of holotype with inner side of A and B ray arms exhibiting deep groove, NMVP390, ×3

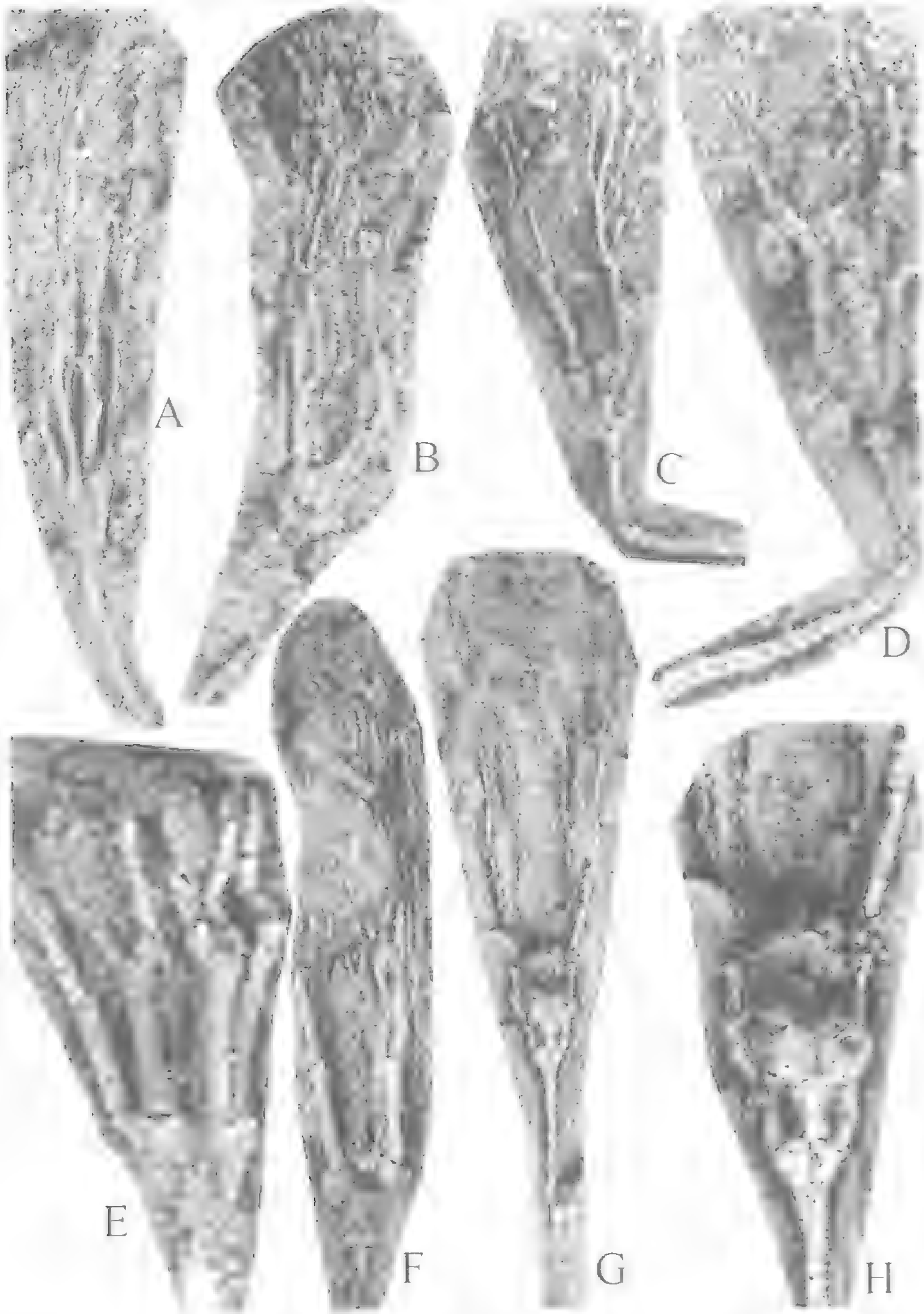


FIG. 80. *Nassoviocrinus corcorani* sp. nov all crowns in lateral view; A,G,H from NMVPL299; B-F, from NMVPL2259. A, NMVP109207, ×3. B, NMVP59498, ×7. C,D, part and counterpart of holotype NMVP109202, ×4 and ×5, respectively. E, NMVP149363. F, NMVP109199, ×7. G,H, NMVP148575, ×2 and ×4, respectively.

pentastellate stem, isotomous arm branching and peneplenary radial facets. It is distinguished from the type and other species of the genus by having unornamented thecal plates.

This, along with *N. corcorani*, is the first record of the genus from the Silurian and the depressed corners of thecal plates in the latter species indicate that the main lineage with thecal ornament began before the Ludlow and that *N. longibrachiatus* was an early offshoot that evolved a smooth theca.

**Nassoviocrinus corcorani** sp. nov.
(Fig. 80)

Class Crinoidea Talent, 1965:17, pl. 4, fig. 2.

ETYMOLOGY. For Peter Corcoran of Sandringham, Melbourne who contributed material to this study.

MATERIAL. HOLOTYPE: NMVP109202 from NMVPL2259. PARATYPES: NMVP59498, 109199, 149363 from NMVPL2259; NMVP109207, 148575 from NMVPL299.

DIAGNOSIS. Cup high conical; thecal plates with broad low ridge ornament leaving corners of plates depressed; radial facet peneplenary; radianal quadrangular; arms branching isotomously, at least 3 times; stem pentagonal in section, heteromorphic.

DESCRIPTION. Crown 20mm long, subcylindrical. Cup high conical, longer than wide. Thecal plates with 2 broad low ridges running diagonally distally from the basal corners of infrabasals to cross on infrabasals and basals and then meet another such ridge at the base of the radial facet. Infrabasals 5, pentagonal, longer than wide, with lateral proximal corners projecting slightly where they extend onto the projections in the stem. Basals 5, hexagonal, longer than wide, largest plates in cup. Radials 5, pentagonal, longer than wide; radial facet peneplenary, subcircular, horizontal or almost so. Anal plates in cup 2; radianal quadrangular, proximal and left of C radial; anal X longer than wide, in radial circlet. Anal sac unknown. Arms isotomous, branching at least 3 times, deep U-shaped in section (i.e. laterally compressed), with deep groove on inner side; primibrach 5 or 6 axillary; 2nd and 3rd branchings may be at different levels in same arm. Stem pentagonal, noditaxis N212, with alternating long nodals and short internodals.

REMARKS. This species is distinguished by its high conical cup although plate boundaries are poorly defined in some specimens, its broad low ridge ornament, its quadrangular radianal, peneplenary horizontal radial facets and its pentagonal stem of very small diameter. It is a much smaller species than others in the genus and has a taller cup but its stem and posterior interray are quite compatible with *Nassoviocrinus*.

**Dictenocrinus** Jaekel, 1918

TYPE SPECIES. *Botryocrinus decadactylus* Bather, 1891 from the Upper Silurian of England.

**Dictenocrinus ibaeypus** sp. nov.
(Fig. 81)

ETYMOLOGY. Ib = infrabasal and Greek *aipys*, tall.

MATERIAL. HOLOTYPE: NMVP108612. PARATYPES: NMVP108624, 108635, 108649, 108657, 108680, 108682, 149373 from NMVPL252.

DIAGNOSIS. Cup high conical; thecal plates smooth; infrabasals long, longer than wide; radial facets peneplenary, horizontal; radianal quadrangular; anal tube tall, straight, of smooth hexagonal plates; arms 10, isotomous, pinnulate, with 3rd or 4th primibrach axillary; stem circular in section, heteromorphic.

DESCRIPTION. Crown subcylindrical, 35mm long. Cup high conical, longer than wide. Thecal plates smooth. Infrabasals 5, pentagonal, upto twice as long as wide, only gently upflared, fully visible laterally except for lower flange resting on stem. Basals 5, largest plates in cup, twice as long as wide; posterior basal 7-sided, supporting the anal X distally and slightly to the right across a slightly oblique suture. Radials 5, pentagonal, as long as wide; radial facet, peneplenary, round, subhorizontal, not declined. Two anal plates in cup: radianal quadrangular, proximal and left of C radial; anal X in radial circlet, same size and shape as radials, distal edge distal to top of D radial but same level as top of C radial. Anal sac long, of alternating vertical columns of small smooth plates, tip unknown. Arms isotomous, deep, narrow, U-shaped cross section, dividing only once on 3rd or 4th primibrach, uniserial with rectangular brachials in proximal parts becoming slightly cuneate distally, with deep V-shaped furrow on inner side, with long fine pinnules one per brachial alternating from side to side up each arm, pinnules apparently absent from primibrachs including axillary. Stem circular in section, noditaxis N1, with nodals at least twice as long as and slightly wider than internodals, with fine central canal.

REMARKS. Within the genus the length of the infrabasals coupled with smooth anal plates and

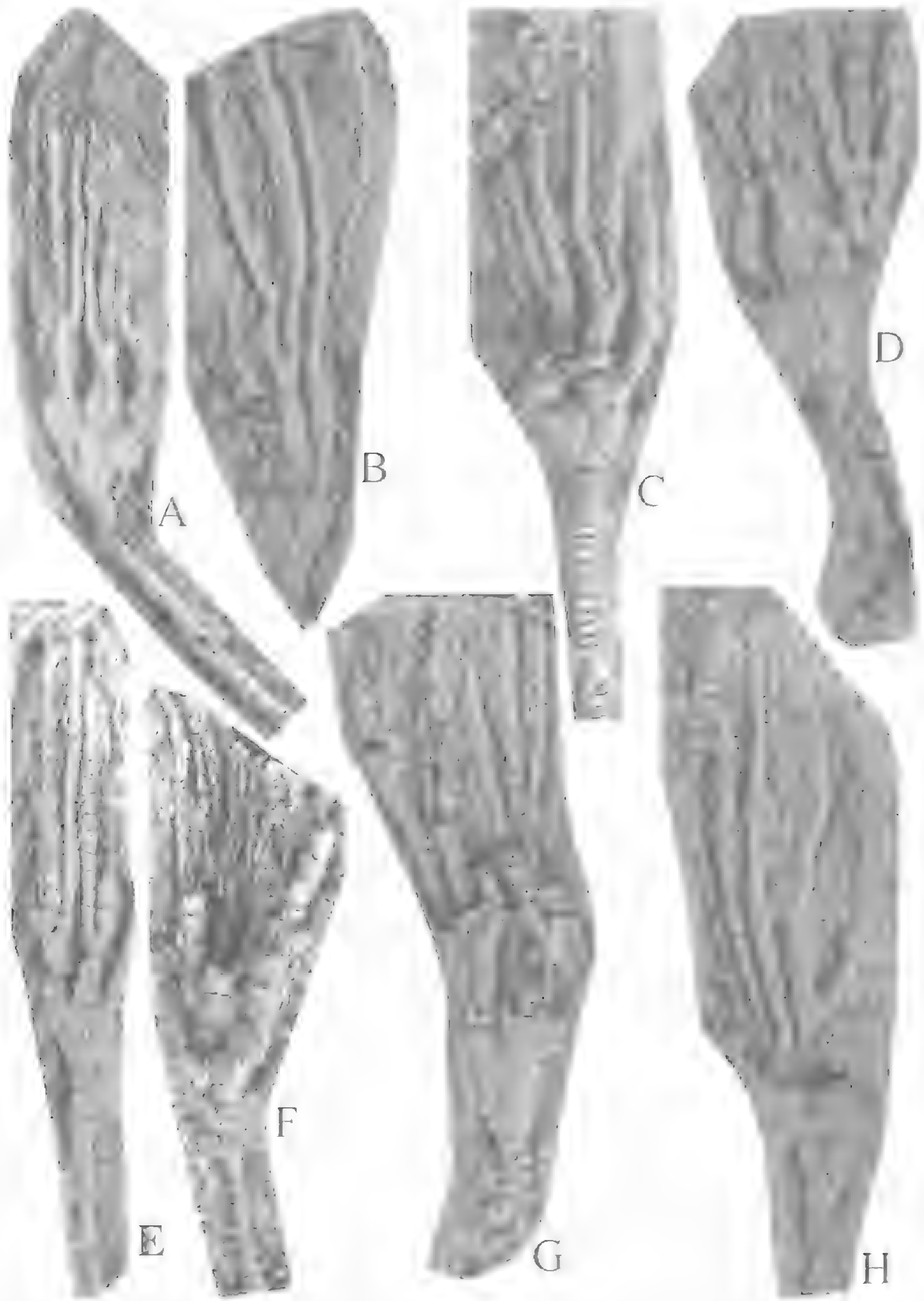


FIG. 81. *Dictenocrinus ibaeypus* sp. nov., all lateral views of crowns from NMVPL252. A, NMVP108657, ×3. B, NMVP149373, ×3. C, NMVP108624, ×3. D, posterior view of holotype NMVP108612, ×3. E, NMVP108682b, ×3. F, NMVP108680, ×3. G, NMVP108635, ×3. H, NMVP108649, ×3.

round stem separate all except *D. cyathiformis* (Haarmann, 1921). *D. cyathiformis* is only distinguished by its stem having uniform columnals and expanding proximally to base of cup, by its anal X being 6-sided and by its shorter pinnules.

**Dictenocrinus remotus** sp. nov.
(Fig. 82B)

ETYMOLOGY. Latin *remotus*, distant; the material was collected a long way from where it occurred because the material was excavated at Coldstream West Road and taken down Mooroolbark Road to fill a large depression.

MATERIAL. HOLOTYPE: NMVP149374 from NMVPL1990.

DIAGNOSIS. Low conical cup, of convex plates; radial facets peneplenary; anal tube tall, of plicate plates; radianal subquadrate, proximal and left of C radial; arms heterotomous, with one main division in each ray on axillary 3rd primibrach, with long nonpinnulate ramules on every 3rd or 4th brachial distal to the first division; stem pentagonal in section, heteromorphic.

DESCRIPTION. Crown subcylindrical, 35mm long. Cup low conical, as long as wide. Thecal plates convex, smooth. Infrabasals 5, pentagonal, short (slightly wider than long), fully visible laterally. Basals 5, large, hexagonal; posterior basal 7-sided, supporting the anal X distally. Radials 5, pentagonal, as long as wide; radial facet, peneplenary, round, declivate at very low angle. Two anal plates in cup; radianal subquadrate, proximal and left of C radial; anal X in radial circlet, same size and shape as radials, distal margin in line with distal margin of C and D radials. Anal sac tall, of vertical columns of small plicate plates, tip unknown. Arms heterotomous, with narrow, U-shaped cross section, with one main division at 3rd primibrach, uniserial with long rectangular brachials proximally becoming slightly cuneate distally, with long nonpinnulate ramules on every 3rd or 4th brachial distally. Stem pentagonal in section, heteromorphic, with noditaxis N3231323.

REMARKS. Although known from only one specimen this species has the single main division of ramulate arms and pentagonal stem found in the type species (Bather,1891) from which it is distinguished by the plicate anal tube and peneplenary radial facets.


FIG. 82. A, *Dictenocrinus* sp. cf. *D. ibaeypus* sp. nov., anterior lateral view of crown NMVP107058 from a road cutting on the road to Wonga Park, east of Melbourne, ×3. B, *Dictenocrinus remotus* sp. nov. posterior view of crown NMVP149374 from NMVPL1990 (although collected from spoil heap on Mooroolbark Road), ×3

**Dictenocrinus** sp. cf **D. ibaeypus** sp. nov.
(Fig. 82)

MATERIAL. NMVP107058 from a road cutting on the road to Wonga Park in eastern Melbourne.

DESCRIPTION. Crown subcylindrical, 40mm long. Cup high conical, longer than wide. Thecal plates smooth. Basals largest plates in cup, twice as long as wide. Radials 5, pentagonal, as long as wide; radial facet angustary, round, subhorizontal. Arms isotomous, U-shaped cross section, dividing once on 3rd or 4th primibrach, uniserial, with rectangular brachials proximally becoming cuneate distally, with long fine pinnules 1 per

brachial alternating from side to side along each arm, pinnules apparently absent from primibrachs including axillary. Stem not known.

REMARKS. This specimen differs from *D. ibaeypus* in its radial facet being more angustary than peneplenary and in its secundibrachs being cuneate. Without knowledge of the posterior interradius it is not possible to assign this specimen with certainty but if the posterior was identical with *D. ibaeypus* the variations noted above might well be considered to be intraspecific variation particularly since the 2 populations represented occurred some 40-50km apart.

Subclass FLEXIBILIA Zittel, 1895
Order TAXOCRINIDA Springer, 1913
Family TAXOCRINIDAE Angelin, 1878

**Meristocrinus** Springer, 1906

TYPE SPECIES. *Taxocrinus loveni* Wachsmuth & Springer, 1880 (=*Cyathocrinus interbrachiatus* Angelin, 1878) from the Upper Silurian of Gotland, Sweden; by original designation.

**Meristocrinus quatriramus** sp. nov.
(Fig. 83)

ETYMOLOGY. Latin *quatri-*, four and *ramus*, branch; for the 4 branchings of each arm.

MATERIAL. HOLOTYPE: NMVP109765 from NMVPL1924.

DIAGNOSIS. Infrabasals evident laterally anteriorly but not posteriorly. C ray with radianal in inferoradial position. Arms branching 4 times. Stem of uniform diameter, proximally of short uniform plates becoming heteromorphic distally.

DESCRIPTION. Crown inverted pear-shaped, 60mm long. Cup small, low bowl-shaped, flaring strongly. Infrabasals visible in lateral view as short circlet with low peaks at 3 way junctions with 2 adjoining basals, number not determinable, may be fused. Basals 5, hexagonal, in AB and probably CD and DE interrays, pentagonal in AE and probably BC interrays, with short vertical sides, with highly obtuse or no basal angle and upper angle of 90°; CD basal irregular, with projection extending distally between D radial and radianal, with radianal in inferoradial position beneath C ray. Radials pentagonal, with plenary facets. Arms long, isotomous, expanding above radials, branching on primibrach 3, secundibrach 4, tertibrach 5 and quaternibrach 6, without interprimibrachs but with single pentagonal intersecundibrach (visible from inner side of arms), wide shallow groove on inner surface becoming deeper and occupying more of the arm width distally. Stem circular in section, widest proximally, of short, strongly crenulate columnals proximally, becoming heteromorphic distally with nodals and internodals alternating in length but uniform in diameter.

REMARKS. The posterior interray is not well preserved and is apparently distorted. The radianal is interpreted to be beneath the C radial and is drawn (Fig. 83B) as it appears as 2 separate pieces but this is probably due to preservation. More distal anal plating is very unclear. Among the 5 species recognised in this genus only *M. tuberosus* Springer, 1920 from the Wenlock of Gotland has arms that divide 4 times but it has only 3 secundibrachs as opposed to 4 in this Australian species.

**Quadritaxocrinus** gen nov.

TYPE SPECIES. *Quadritaxocrinus websteri* sp. nov.

ETYMOLOGY. Latin *quadri-*, four and generic name *Taxocrinus*.

DIAGNOSIS. Cup small; infrabasals not visible in lateral view; primibrachs 4; arms branching isotomously at 1st division, with 3rd divisions on inner branches at same level and those on outer branches at same level but more distal than on inner branches; stem circular in section, of short columnals proximally.

REMARKS. This genus compares closely with *Taxocrinus* in the infrabasals concealed by the stem, the wide posterior basal extending up between the C and D radials, shape of the axillary brachials and the lipped interbrachial articulations. Among Taxocrinidae the number of primibrachs is consistent at the generic level. *Taxocrinus*, with which *Quadritaxocrinus* is most closely allied, has 3 primibrachs and I suggest that evolution from the former to the latter in the Lower Devonian involved introduction of an extra primibrach. Ubaghs (1978a) pointed out that all Ordovician and Silurian, most Devonian and some Carboniferous genera have 2 primibrachs and from the Carboniferous on 3 is the standard number. More than 3 primibrachs are known in some species of *Onychocrinus* (Synerocrinidae) but that genus has entirely different arms from the new Australian taxon. The obvious inference is that the number of primibrachs increases with evolution in the flexible crinoids so evolution to 4


FIG. 83. *Meristocrinus quatriramus* sp. nov., large crown NMVP109765, from NMVPL1924. A, closeup of cup in posterior view, ×4. B, sketch of plate arrangement of A. C, posterior view of crown, ×1.5. D, interior of arms, ×4. E, anterior view of crown, ×2

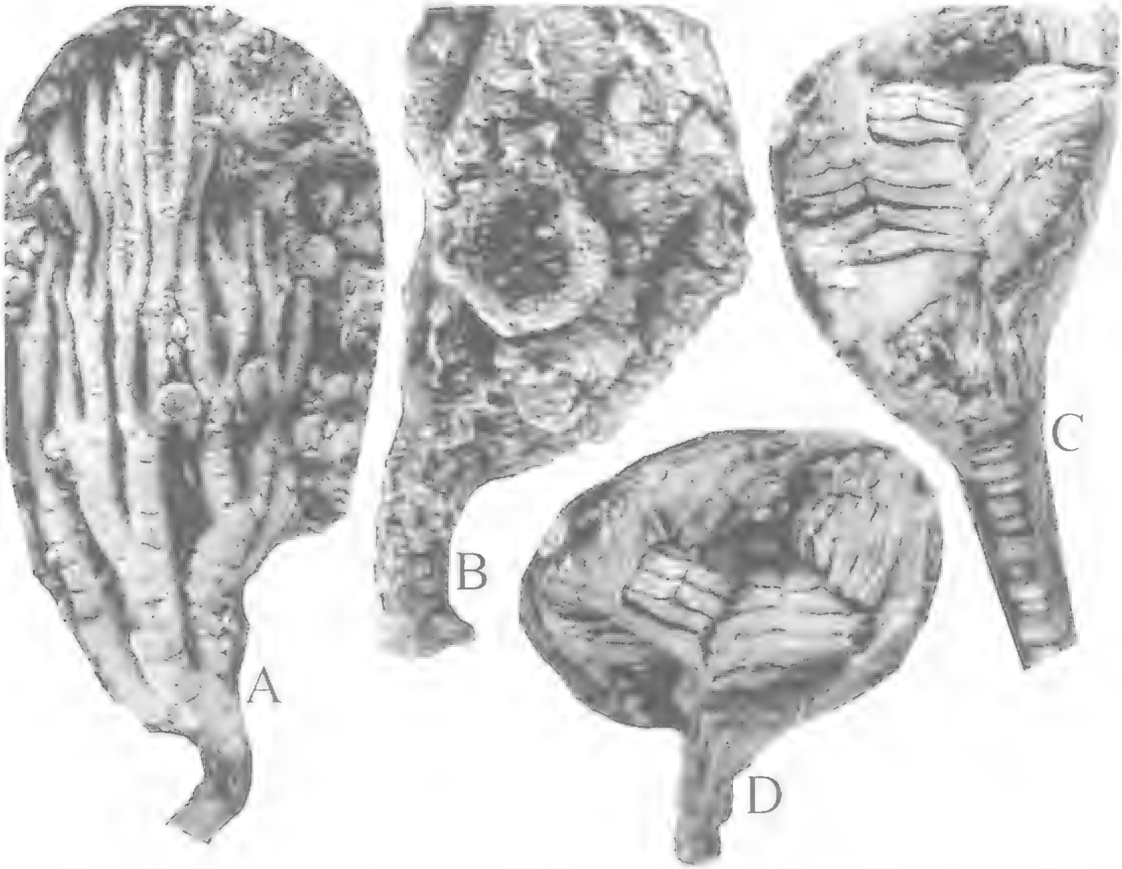


FIG. 84. A,B, *Quadritaxocrinus websteri* gen. et sp. nov., holotype crown NMVP149354 from NMVPL6601. A, E ray view, ×3. B, C ray view with circular columnal concealing CD interray above anal X, ×5. C,D, *Geroldicrinus* sp., crown NMVP149362 from NMVPL1990, ×3. C, lateral anterior view. D, distal view.

primibrachs in *Quadritaxocrinus* is not unexpected even if it is the first record of such increase in the Taxocrinidae.

**Quadritaxocrinus websteri** sp. nov.
(Fig. 84A, B)

ETYMOLOGY. For Gary D. Webster, Washington State University who provided many useful discussions on crinoids.

MATERIAL. HOLOTYPE: NMVP149354 from NMVPL6601.

DIAGNOSIS. As for genus.

DESCRIPTION. Crown 35mm long. Infrabasals concealed by stem. Basals not clearly defined but probably 5, wider than long; CD basal irregular in shape, with projection extending up between C and D radials. Radials pentagonal, with plenary facets. Arms long, dividing isotomously on 4th primibrach, with next division at secundibrach 4 producing unequal branches, with 3rd and 4th divisions at different levels, without interprimibrachs. Stem circular in section, widest proximally, of short, strongly crenulate columnals proximally.

REMARKS. The only available specimen is not clear in definition of the cup plates but the proximal and distal margins of the basals, with the posterior basal extending up between the C and D radials and outline of the radials are clear.

Order SAGENOCRINIDA Springer, 1913
Family LECANOCRINIDAE Springer, 1913

**Geroldicrinus** Jaekel, 1918

TYPE SPECIES. *Lecanocrinus roemeri* Schultze, 1867 from the Middle Devonian of Germany.

### **Geroldicrinus** sp.
(Fig. 84C, D)

MATERIAL. NMVP149362 from NMVPL1990.

DESCRIPTION. Crown 15mm long, egg-shaped but truncated distally, crushed and therefore, not useful in comparing dimensions. Cup, conical, of smooth plates, but only the distal part of 1 anterior radial available. Infrabasals and basals not evident. Arms plenary, with 1st primibrach axillary, with 1 further division at different levels in same ray, closely abutting each other laterally, strongly incurved distally to fully enclose a space distal to the cup. Stem circular in section, of short columnals proximally, becoming longer and heteromorphic distally.

REMARKS. Even though anal plating at the posterior and the lower cup are not available crown shape, arm branching and structure and particularly the axillary 1st primibrach are sufficient to identify this genus. Since Schultze (1867) described this genus it has not been recognised elsewhere and so this single specimen from Victoria is a significant range extension.

## STEM ONLY
Group PENTAMERATA Stukalina, 1966
Order STRIALATA Stukalina, 1978
Family DECACRINIDAE Yeltyschewa, 1957

### **Decacrinus** Yeltyschewa, 1957

TYPE SPECIES. *Decacrinus pennatus* Yeltyschewa, 1957 from the Lower Devonian of central Kazakhstan.

### **Decacrinus** sp.
(Fig. 85)

MATERIAL. NMVP149353 from NMVPL1924.

REMARKS. This form genus is distinctive in having 5 grooves radiating from the central canal towards the 5 outer angles of the stem as well as 5 shorter but wider grooves radiating from the central canal towards the middle of each side of the stem. Stukalina (1986) recorded this genus in the Early Devonian (Gedinnian and Siegennian) which is the same age as the Australian specimen. Species identification of the Australian specimen is not attempted because it does not fit easily into a known species and I am reluctant to erect a new one on a single specimen without knowing the crown it supported. The projections at the 5 angles are very reminiscent of the stem of Pterinocrinidae gen. nov., described above, from the Lilydale area but preservation of that specimen is not good enough for certain identification.

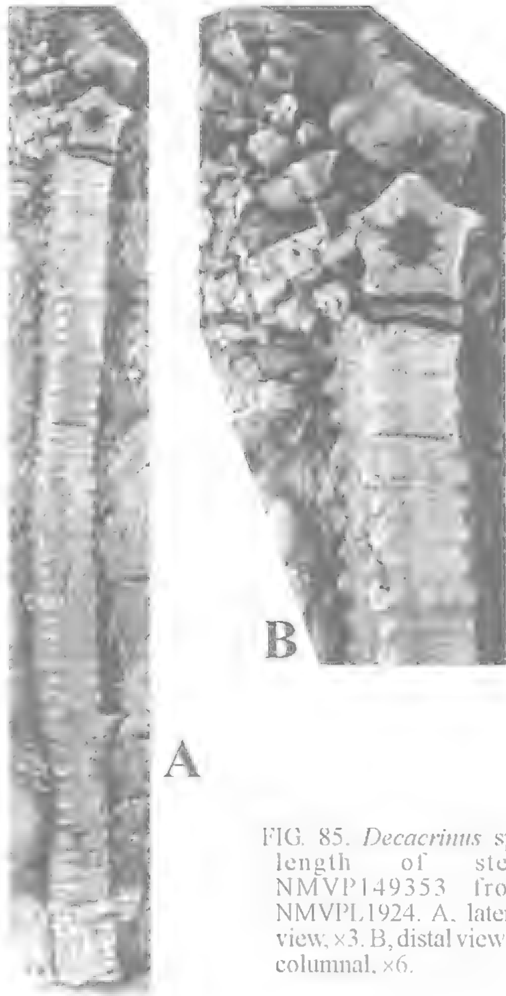


FIG. 85. *Decacrinus* sp., length of stem NMVP149353 from NMVPL1924. A, lateral view, ×3. B, distal view of columnal, ×6.

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## LITERATURE CITED

ANGELIN, N.P. 1878. Iconographia crinoideorum in stratis Sueciae Siluricus fossilium. (Samson & Wallin: Holmiae). 62p.

ARENDT, Yu. A. 1965. K poznaniyu morskihh lilii kaltseokrinid [Contribution to the knowledge of crinoids from the Family Calceocrinidae]. Paleontologicheskii Zhurnal 1965(1): 90-96.

AUSICH, W.I. 1986a. Early Silurian Rhodocrinitacean crinoids (Brassfield Formation, Ohio). Journal of Paleontology 60: 84-106.

1986b. New camerate crinoids of the Suborder Glyptocrinina from the Lower Silurian Brassfield Formation (Southwestern Ohio). Journal of Paleontology 60: 887-897.

1987. Brassfield Compsocrinina (Lower Silurian crinoids) from Ohio. Journal of Paleontology 61: 552-562.

AUSICH, W.I. & DRAVAGE, P. 1988. Crinoids from the Brassfield Formation of Adams County, Ohio. Journal of Paleontology 62: 285-289.

AUSTIN, T. & AUSTIN, T. Jr 1843. XXXIII. Description of several new genera and species of Crinoidea. Annals and Magazine of Natural History, series 1, 11(69): 195-207.

BATES, D.E.B. 1972. A new Devonian crinoid from Australia. Palaeontology 15: 326-335.

BATHER, F.A. 1891. British fossil crinoids. 5. *Botryocrinus*, Wenlock Limestone. Annals and Magazine of Natural History 67: 389-423.

1893. The Crinoidea of Gotland, Part 1, the Crinoidea Inadunata. Kongliga Svenska Vetenskaps-akademiens Handlingar 25(2): 1-182.

1897. *Hapalocrinus victoriae*, n.s., Silurian, Melbourne, and its relation to the Platycrinidae. Geological Magazine, Decade 4, 4: 337-345.

BILLINGS, E. 1857. On the Crinoidea or stone lilies of the Trenton Limestone, with a description of a new species. Canadian Naturalist and Geologist, series 1, 1: 48-57.

BLANDOWSKI, W. 1855. A description of fossil animalculae in primitive rocks from the Upper Yarra district. Transactions of the Philosophical Society of Victoria 1: 221-223.

BOUCOT, A.J., JOHNSON, J.G. & TALENT, J.A. 1969. Early Devonian brachiopod zoogeography. Special Papers of the Geological Society of America 119:1-107.

BOUSKA, J. 1947. *Pygmaeocrinus*, a new crinoid from the Devonian of Bohemia. Vestnik Kralovske ceske spolecnosti nauk, Trida 2 (mathematicko-prirodovedna) 1946: 1-4.

BREIMER, A. 1962. A monograph of Spanish Palaeozoic Crinoidea. Leidse Geologische Mededelingen 27: 1-190.

BRETT, C.E. 1981. Systematics and paleoecology of Late Silurian (Wenlockian) calceocrinid crinoids from New York and Ontario. Journal of Paleontology 55: 145-175.

BRONN, H.G. 1840. *Ctenocrinus*, ein neues Krinoiden-Geschlecht der Grauwacke. Neues Jahrbuch Mineralogie, Geologie, Paläontologie 542-548.

BROWER, J.C. 1973. Crinoids from the Girardeau Limestone (Ordovician). Palaeontographica Americana 7: 261-499.

1976. Evolution of the Melocrinitidae. Thalassia Jugoslavica 12: 41-49.

1992. Cupulocrinid crinoids from the Middle Ordovician (Galena Group, Dunleith Formation) of northern Iowa and southern Minnesota. Journal of Paleontology 66: 99-128.

1995. Dendrocrinid crinoids from the Ordovician of northern Iowa and southern Minnesota. Journal of Paleontology 69: 939-960.

CAS, R. 1983. Palaeogeographic and tectonic development of the Lachlan Fold Belt, southeastern Australia. Geological Society of Australia Special Publication 10: 1-104.

CHAPMAN, F. 1903. New or little known fossils in the National Museum, Melbourne. Part 1. Some Palaeozoic species. Proceedings of the Royal Society of Victoria new series 15: 104-122.

1934. New species of a crinoid (*Lecanocrinus*) and a cephalopod (*Ophidioceras*), from the Silurian of Yass. Proceedings of the Royal Society of Victoria, new series 47: 190-195.

ECKERT, J.D. 1984. Early Llandovery crinoids and stelleroids from the Cataract Group (Lower Silurian) in southern Ontario, Canada. Royal Ontario Museum Life Sciences Contributions 137: 1-83.

ECKERT, J.D. & BRETT, C.E. 1985. Taxonomy and palaeoecology of the Silurian myelodactylid crinoid *Crinobrachiatus brachiatus* (Hall). Royal Ontario Museum Life Sciences Contributions 141: 1-15.

ETHERIDGE, R. Jr 1904. The occurrence of *Pisocrinus* or an allied genus, in the Upper Silurian rocks of the Yass district. Records of the Australian Museum 5(5): 287-292.

FOLLMANN, O. 1887. Unterdevonische Crinoiden. Verhandlungen des naturhistorischen Vereines der preussischen Rhinelande, Westfalens und des Reg.-Bezirks Osnabrück series 5 4: 113-138.

FREST, T.J. & STRIMPLE, H.L. 1981. New camerate crinoids from the Silurian of North America. Journal of Paleontology 55: 639- 655.

GARRATT, M.J. 1983. Silurian and Devonian biostratigraphy of the Melbourne Trough, Victoria. Proceedings of the Royal Society of Victoria, new series 95: 77-98.

GARRATT, M.J. & WRIGHT, A.J. 1988. Late Silurian to Early Devonian biostratigraphy of southeastern Australia. Pp. 647-662. In McMillan, N.J., Embrey, A.F. & Glass, D.J. (eds) Devonian of the World, Vol. 3. (Canadian Society of Petroleum Geologists: Calgary).

GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology 41: 1-71.

GOLDRING, W. 1923. The Devonian crinoids of the State of New York. Memoirs of the New York State Museum 16: 1-670.

HAARMANN, E. 1921. Die Botryocriniden und Lophocriniden des rheinischen Devons. Sonderabdruck aus dem Jahrbuch der Preussischen Geologischen Landesanstalt 41(1): 1-87.

HALL, J. 1847. Palaeontology of New York, vol. 1, containing descriptions of the organic remains of the lower division of the New York System (equivalent of the Lower Silurian rocks of Europe). Natural History of New York 6: 1-338.

1852. Palaeontology of New York, vol. 2, containing descriptions of the organic remains of the lower middle division of the New York System. Natural History of New York 6: 1-362.

1863. Notice of some new species of fossils from a locality of the Niagara Group, in Indiana; with a list of identified species from the same place. Transactions of the Albany Institute 4: 195-228.

1872. Description of new species of Crinoidea and other fossils from strata of the age of the Hudson River Group and Trenton Limestone. Annual Report of the New York State Museum of Natural History 24: 205-224.

HAUDE, R. 1995. Lower Devonian echinoderms from the Precordillera (Argentina). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 197: 37-86.

HISINGER, 1840. Lethaea Suecica, seu petrificata Sueciae, iconibus et characteribus illustrata. Supplementum secundum, pp. 1-11, pls 38, 39.

JAEKEL, O. 1895. Bietrage zur kenntnis der palaeozoischen Crinoiden Deutschlands. Palaeontologisches Abhandlungen, new series 3: 1-116.

1898. Über einige paläontologische Gattungen von Crinoiden. Deutsche Geologisches Gesellshafte Zeitschrift Verhandlingen 49: 44-48.

1918. Phylogenie und System der Pelmatozoen. Palaeontologische Zeitschrift 3: 1-128.

JELL, P.A. 1982. *Crotalocrinites pulcher* (Hisinger, 1840) from the Early Devonian of central Victoria. Alcheringa 6: 174.

1983. Early Devonian echinoderms from Victoria (Rhombifera, Blastoidea and Ophiocystioidea). Memoirs of the Association of Australasian Palaeontologists 1: 209-235.

JELL, P.A. & JELL, J.S. 1999. Crinoids, a blastoid and a cyclocystoid from the Upper Devonian reef complex of the Canning Basin, Western Australia. Memoirs of the Queensland Museum 43:201-236.

JELL, P.A. & HOLLOWAY, D.J. 1983. Devonian and ?Late Silurian palaeontology of the Winneke Reservoir site, Christmas Hills, Victoria. Proceedings of the Royal Society of Victoria 95: 1-21.

JELL, P.A., JELL, J.S., JOHNSON, B.D., MAWSON, R. & TALENT, J.A. 1988. Crinoids from Devonian limestones of eastern Australia. Memoirs of the Queensland Museum 25: 355-402.

JELL, P.A. & THERON, J.N. 1999. Early Devonian echinoderms of South Africa. Memoirs of the Queensland Museum 43: 115-199.

JOBSON, L. & PAUL, C.R.C. 1979. *Compagicrinus fenestratus*, a new Lower Ordovician inadunate crinoid from North Greenland. Rapport Gronlands Geologic Undersag 91: 1-81.

KESLING, R.V. 1964. A new species of *Melocrinites* from the Middle Devonian of Michigan. University of Michigan Contributions from the Museum of Paleontology 19: 89-103.

1966. *Botryocrinus niemani*, a new crinoid from the Middle Devonian Silica Formation of Ohio. University of Michigan Contributions from the Museum of Paleontology 20: 271-276.

1968. *Ameliacrinus benderi*, a new dicyclic camerate crinoid from the Middle Devonian Silica Formation in northwestern Ohio. University of Michigan Contributions from the Museum of Paleontology 22: 155-162.

KESLING, R.V. & CHILMAN, R.B. 1975. Strata and megafossils of the Middle Devonian Silica Formation. University of Michigan, Museum of Paleontology, Papers on Paleontology 8: 1-408.

KIER, P.M. 1952. Echinoderms of the Middle Devonian Silica Formation of Ohio. Contributions from the Museum of Paleontology at the University of Michigan 10: 59-81.

KIRK, E. 1914. Notes on the fossil crinoid genus *Homocrinus* Hall. Proceedings of the United States National Museum 46: 473-483.

1929. The status of the genus *Mariacrinus* Hall. American Journal of Science 17: 337-346.

1945. Four new genera of camerate crinoids from the Devonian. American Journal of Science 243: 341-355.

KOLATA, D.R. 1975. Middle Ordovician echinoderms from northern Illinois and southern Wisconsin. Memoirs of the Paleontological Society 7: 1-74.

LEMENN, J. 1975. Un nouveau genre d'Hexacrinitidae (Crinoidea, Camerata). Annales de la Societé Géologique du Nord 95: 243-250.

1985. Les Crinöides du Dévonien Inférieur et Moyen du Massif Armoricain. Mémoires de la Societé Géologique et Minéralogique de Bretagne 30: 1-268.

McINTOSH, G.C. 1979. Abnormal specimens of the Middle Devonian crinoid *Bactrocrinites* and their effect on the taxonomy of the genus. Journal of Paleontology 53: 18-28.

1981. *Apurocrinus sucrei*, a new genus and species of camerate crinoid from the Lower Devonian of Bolivia. Journal of Paleontology 55: 948-952.

1983. Review of the Devonian cladid inadunate crinoids: Suborder Dendrocrinina. PhD Thesis, Univ. Michigan, 521p.

1986. Phylogeny of the dicyclic inadunate crinoid Order Cladida. Abstracts from the 4th North American Paleontological Convention.

1987. Review of the Devonian camerate crinoid *Bogotacrinus scheibei* Schmidt from Colombia. Journal of Paleontology 61: 750-757.

MEEK, F.B. & WORTHEN, A.H. 1869. Descriptions of new Crinoidea and Echinoidea from the Carboniferous rocks of the western states, with a note on the genus *Onychaster*. Proceedings of the Academy of Natural Sciences of Philadelphia 21: 67-83.

MILITSINA, V.S. 1980. Cystoidea and Crinoidea from the Ordovician and Silurian of the Urals. Ezhegodnik Bsesoyoznogo Paleontologicheskogo Obshchestva 23: 198-215.

MILLER, J.S. 1821. A natural history of the Crinoidea or lily-shaped animals, with observations on the genera *Asteria*, *Euryale*, *Comatula*, and *Marsupites*. (Bryan & Co.: Bristol).

MILLER, S.A. & GURLEY, W.F.E. 1895 New and interesting species of Palaeozoic fossils. Bulletin of the Illinois State Museum of Natural History 7: 1-89.

MOORE, R.C. 1962. Revision of Calceocrinidae. University of Kansas, Paleontological Contributions, Article 4: 1-40.

MOORE, R.C., LANE, N.G. & STRIMPLE, H.L., 1978. Order Cladida. Pp. T578-T759. In Moore, R.C. & Teichert, C. (eds) Treatise on invertebrate paleontology, Part T, Echinodermata 2. (Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas).

MOORE, R.C., LANE, N.G., STRIMPLE, H.L. & SPRINKLE, J., 1978. Order Disparida. Pp. T520-577. In Moore, R.C. & Teichert, C. (eds) Treatise on invertebrate paleontology, Part T, Echinodermata 2. (Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas).

MOORE, R.C. & TEICHERT, C. (eds) 1978. Treatise on invertebrate paleontology, Part T, Echinodermata 2 (3 vols). (Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas).

MULLER, J. 1856. Über neue Crinoiden aus dem Eifeler Kalk. Koniglich Akademie der Wissenschaft Berlin, Monatsbericht 1856: 353-356.

MUNSTER, G.G. 1839. Beschreibung einiger neuen Crinoideen aus der Uebergangs-formation. Beitrage zur Petrefaten-Kunde 1: 31-34.

MURCHISON, R.I. 1839. The Silurian System, Part 1. Founded on researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmonth, Gloucester, Worcester, and Stafford; with descriptions of the coalfields and overlying formations. 578p; Part 2. Organic remains. 579-768. (John Murray: London).

d'ORBIGNY, 1850. Prodrome du paléontologie stratigraphique universelle des animaux mollusques et rayonnes faisant suite au cours elementaire de paleontologie et de geologie stratigraphique. Vol. 1. (Masson: Paris).

PHILIP, G.M. 1961. Lower Devonian crinoids from Toongabbie, Victoria, Australia. Geological Magazine 98: 143-160.

PHILIP, G.M. & STRIMPLE, H.L. 1971. An interpretation of the crinoid *Aethocrinus moorei* Ubaghs. Journal of Paleontology 45: 491-493.

PHILLIPS, J. 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset. (Longman, Brown, Green & Longmans: London).

PROKOP, R.J. 1970. Family Calceocrinidae Meek & Worthen, 1869 (Crinoidea) in the Silurian and Devonian of Bohemia. Sbornik Geologickych Ved, Rada P 12: 79-134.

1982. Some new hexacrinitids (Crinoidea, Camerata) from the Lower Devonian of Bohemia. Vestnik Ustredniho Ustavu Geologickeho 57: 277-284.

1973. *Elicrinus* n. gen. from the Lower Devonian of Bohemia (Crinoidea). Vestnik Ustredniho Ustavu Geologickeho 48: 221-224.

PROKOP, R.J. & PETR, V. 1997. The genus *Pygmaeocrinus* Bouska, 1947 (Crinoidea, Inadunata) in the Devonian of the Barrandian area (Czech Republic). Acta Musei Nationalis Pragae, Series B, Historia Naturalis 53: 1-10.

RAMSBOTTOM, W.H.C. 1961. A monograph on British Ordovician Crinoidea. Palaeontographical Society Monograph 114: 1-37.

RINGUEBERG, E.N.S. 1888. Some new species of fossils from the Niagara shales of western New York. Academy of Natural Sciences of Philadelphia Proceedings for 1888: 131-137.

ROEMER, C.F. 1855. Erste Periode, Kohlen-Gebirge. In Bronn, H.G. Lethaea Geognostica, vol. 2 (3rd ed.) (E. Schweizerbart: Stuttgart).

ROZHNOV, S.V. 1981. Crinoids of the Superfamily Pisocrinacea. Trudy Paleontological Institute 192: 1-127.

SALTER, J.W. 1856. Description of Palaeozoic Crustacea and Radiata from South Africa. Transactions of the Geological Society of London 7: 215-224.

SCHMIDT, W.E. 1913. Cultrijugatuszone und unteres Mitteldevon sudlich der Attendorn-Elsper

Doppelmulde. K. Preussen Geologisches Landesanst. Jahrbuch 33(2): 265-318.

1934. Die Crinoideen des Rheinischen Devons. Teil 1. Abhandlungen der Preussischen Geologischen Landesanstalt, Neue Folge 163: 1-199.

1941. Die Crinoideen des Rheinischen Devons. Teil 2. Abhandlungen der Reichsstelle für Bodenforschung, Neue Folge 182: 1-253.

SCHULTZE, L. 1867. Monographie der Echinodermen des Eifler Kalkes. Denkschriften der Kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse 26: 113-230.

SHUMARD, B.F. 1855. Description of new species of organic remains. Missouri Geological Survey 2: 185-208.

SPRINGER, F. 1906. Discovery of the disk of *Onychocrinus*, and further remarks on the Crinoidea Flexibilia. Journal of Geology 14: 467-523.

1911. On a Trenton echinoderm fauna at Kirkfield, Ontario. Memoirs of the Geological Survey of Canada 15: 1-69.

1920. The Crinoidea Flexibilia. Smithsonian Institution Publication 2501: 1-486.

1923. On the crinoid Family Catillocrinidae. Smithsonian Miscellaneous Collections 76(3): 1-41.

1926. American Silurian crinoids. Publications of the United States National Museum 2871: 1-240.

STEWART, G.A., 1940. Crinoids from the Silica Shale, Devonian, of Ohio. Ohio Journal of Science 40: 53-61.

STRIMPLE, H.L. 1963. Crinoids of the Hunton Group (Devonian - Silurian) of Oklahoma. Bulletin of the Oklahoma Geological Survey 100: 1-169.

STRIMPLE, H.L. & LEVORSON, C.O. 1973. Additional crinoid specimens from the Shellrock Formation (Upper Devonian) of Iowa. Proceedings of the Iowa academy of Science 80: 182-184.

STUKALINA, G.A., 1986. Zakonomernosti istoricheskogo razvitiya krinoidei b rannem i crednem paleozoe SSSR [Laws of historical development of crinoidea from the early and middle Paleozoic of the USSR.] (Akademiya Nauk USSR, Paleontological Institute: Moscow).

TALBOT, M. 1905. Revision of the New York Helderbergian crinoids. American Journal of Science, series 4, 20: 17-34.

TALENT, J.A. 1965. The Silurian and Early Devonian faunas of the Heathcote district, Victoria. Memoirs of the Geological Survey of Victoria 26: 1-55.

UBAGHS, G. 1958. Recherches sur les Crinöides Camerata du Silurien de Gotland (Suède). Partie III: Melocrinicae. Avec des remarques sur l'évolution des Melocrinidae. Arkiv för Zoologi series 2, 11: 259-306.

1969. *Aethocrinus moorei* Ubaghs n. gen., n. sp., le plus Ancien Crinoide Dicyclique Connu. University of Kansas Paleontological Contributions, Paper 38: 1-25.

1978a. Skeletal morphology of fossil crinoids. Pp. T58-T216. In Moore, R.C. & Teichert, C. (eds) Treatise on invertebrate paleontology. (Geological Society of America & University of Kansas: Boulder, Colorado & Lawrence, Kansas).

1978b. Camerata Pp. T408-T519. In Moore, R.C. & Teichert, C. (eds) Treatise on invertebrate paleontology. (Geological Society of America & University of Kansas: Boulder, Colorado & Lawrence, Kansas).

VANDENBERG, A.H.M., 1988. Silurian - Middle Devonian. Pp. 103- 146. In Douglas, J.G. & Ferguson, J.A. (eds) Geology of Victoria. (Victorian Division, Geological Society of Australia: Melbourne).

1992. Kilmore 1:50,000 map geological report. Geological Survey of Victoria Report 91: 1-86.

VANDENBERG, A.H.M. & WILKINSON, H.E. 1982. Victoria. In Cooper, R.A. & Grindley, G.W. (eds) Late Proterozoic to Devonian sequences of southeastern Australia, Antarctica and New Zealand and their correlation. Special Publications of the Geological Society of Australia 9: 36-47.

WACHSMUTH, C. & SPRINGER, F. 1880. Revision of the Palaeocrinoidea, part 1. The families Ichthyocrinidae and Cyathocrinidae. Proceedings of the Academy of Natural Sciences of Philadelphia for 1879: 226-378.

1881. Revision of the Palaeocrinoidea, part 2. Family Sphaeroidocrinidae, with the subfamilies Platycrinidae, Rhodocrinidae, and Actinocrinidae. Proceedings of the Academy of Natural Sciences of Philadelphia for 1881: 175-411.

1885. Revision of the Palaeocrinoidea, part 3, section 1. Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions. Proceedings of the Academy of Natural Sciences of Philadelphia for 1885: 223-364.

WILLIAMS, G.E. 1964. The geology of the Kinglake district, central Victoria. Proceedings of the Royal Society of Victoria, new series 77: 273-328.

WILLIAMS, H.S. 1883. On a crinoid with movable spines (*Arthroacantha ithacensis*). American Philosophical Society Proceedings 21: 81-88.

WITHERS, R.B. & KEBLE, R.A. 1934a. The Palaeozoic starfish of Victoria. Proceedings of the Royal Society of Victoria 46: 220-249.

1934b. The Palaeozoic brittlestars of Victoria. Proceedings of the Royal Society of Victoria 47: 196-212.

WITZKE, B.J. & STRIMPLE, H.L. 1981. Early Silurian camerate crinoids of eastern Iowa. Iowa Academy of Science, Proceedings 88: 101-137.

YAKOVLEV, N.N. 1946. Un Hexacrinidae du silurien supérieur. Compte Rendu (Doklady) de Academie des Sciences de l'URSS 51: 153-154.

YELTYSCHEWA, R.S. 1957. O novom semeistwe paleosoiskih morskih lilii. [On a new family of Paleozoic crinoids]. Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva 14: 218-234.

## APPENDIX

List of localities arranged in descending age and grouped as per the columns numbered 1-11 in Figure 1.

**Column 11.** Late *Boucotia australis* Zone (Late Lochkovian).

NMVPL229 Collins Quarry, on access road to youth camp about 2 km N of Tommy's Hut, Kinglake (=X0 of Williams, 1964)
*Hollowaycrinus calvus*
*Eudimerocrinus eckardti*
*Oehlerticrinus lemenni*
*Oehlerticrinus jeani*
*Frankocrinus holmesi*
*Ctenocrinus signatus*
*Ctenocrinus paucidactylus*
*Phimocrinus americanus*
*Antihomocrinus chapmani*
*Ancyrocrinus* sp.
*Kroppocrinus heathcotensis*

NMVPL1924 sandstone bar across Mathieson's Creek about 1km S of Kinglake to Flowerdale Road and about 6km NE of Tommy's Hut (=T95 of Williams, 1964)
*Duncanicrinus calvariolus*
*Eudimerocrinus eckardti*
*Ctenocrinus* sp.
Myelodactylid sp.
*Kroppocrinus mathiesonensis*
*Stewbreecrinus terryi*
*Antihomocrinus chapmani*
*Meristocrinus quatriramus*
*Decacrinus* sp.

**Column 10.** Middle *Boucotia australis* Zone (Late Lochkovian).

Locality R52 of Thomas (1940), Unit 3 Mt Ida Fmn, Parish of Redcastle, N of Heathcote; see Talent (1965, fig. 1)
*Holmesocrinus idaensis*

Locality R25 of Thomas (1940), Unit 3 Mt Ida Fmn, Parish of Redcastle, N of Heathcote; see Talent (1965, fig. 1)
*Crotalocrinites pulcher*
*Ctenocrinus paucidactylus*

**Column 9.** Early *Boucotia australis* Zone (Late Lochkovian).

NMVPL252 Middendorp's Quarry, 2km E of Tommy's Hut, Kinglake (=W3 of Williams, 1964).
*Dimerocrinites bispinosus*
*Eucrinus clarkae*
*Eudimerocrinus eckardti*
*Nexocrinus* sp.
*Duncanicrinus calvariolus*
*Oehlerticrinus lemenni*
*Oehlerticrinus jeani*
*Frankocrinus enidae*
*Ctenocrinus paucidactylus*
*Ctenocrinus stellifer*
*Ctenocrinus signatus*
*Clematocrinus perforatus*
*Darragherinus tomi*
*Codiacrinus secundus*
*Dendrocrinus arrugius*
*Plicodendrocrinus australis*
*Antihomocrinus chapmani*
*Dictenocrinus ibaeypus*

Rubbish tip on Watson's Road at Pheasant Creek, 6km E of Tommy's Hut, Kinglake West.
*Duncanicrinus calvariolus*

**Column 8.** Late *Boucotia janeae* Zone (Early Lochkovian).

NMVPL1990, Road cutting just N of intersection of Victoria Road and Coldstream West Road, 5km N of Lilydale, NE Melbourne.
*Ophiocrinus nnettae*
*Eudimerocrinus gilli*
*Ctenocrinus stellifer*
Pterinocrinidae gen. nov.
*Shintocrinus richi* sp. nov.
*Dictenocrinus remotus* sp. nov.
*Geroldicrinus* sp.

Roadcutting on road (Yarra Road) to Wonga Park, just S of Bryson's Road.
*Dictenocrinus* sp. cf. *D. ibaeypus*

**Column 7.** Middle *Boucotia janeae* Zone (Early Lochkovian).

NMVPL1922 sewerage trench in Kimberley Drive, Chirnside Park, N of Maroondah Highway 3.5km W of Lilydale.
*Hexacrinites chirnsidensis*
*Antihomocrinus chapmani*
*Ctenocrinus stellifer*

**Column 6.** Early *Boucotia janeae* Zone (Early Lochkovian).

NMVPL1841 small excavation on ridge above Ruddock's Quarry (now filled in) W of Edwards Road, 300m NW of its intersection with Switchback Road, Chirnside Park.
*Cupulocrinus austrogracilis*

**Column 5.** Late *Notoparmella plentiensis* Zone (Pridoli).

NMVPL1923 large roadcutting just N of Merriang on Woodstock to Wallan Road, 9km N of Woodstock, 40km N of Melbourne.
*Holmesocrinus enidae*

*Nexocrinus wallanensis*
*Trichocrinus morleyi*

NMVPL260 Excavations for Winneke Dam, 33km NE of Melbourne. (Jell & Holloway, 1983).
*Duncanicrinus calvariolus*
*Kooptoonocrinus nutti*
*Dendrocrinus saundersi*
*Codiacrinus rarus*

**Column 4.** Early *Notoparmella plentiensis* Zone (Late Ludlow).

NMVPL300 near disused mine on Comet Creek, c. 4.6km SE of Clonbinane, 60km N of Melbourne; (=X64 in Clonbinane Sandstone of Williams, 1964).
*Clematocrinus perforatus*
*Alisocrinus lineatus*
*Phimocrinus hanschi*
*Dendrocrinus arrugius*
*Shintocrinus cometensis*
*Antihomocrinus chapmani*

NMVPL6601 on Boundary Road spur above Comet Creek Mine (NMVPL300), 4.6km SE of Clonbinane, 60km N of Melbourne.
*Quadritaxocrinus websteri*

**Column 3.** Late *Aegiria thomasi* Zone (Ludlow).

SW of Bald Hills, just E of railway, N of Sunday Creek Road, 5km E of Kilmore.
*Dendrocrinus arrugius*

NMVPL299 road cutting on Sunday Creek Road, 700m NE of junction with Saunders Lane, Kilmore East (=F31 of Williams, 1964).
*Nassoviocrinus corcorani*
*Trichocrinus morleyi*

**Column 2.** Late *Aegiria thomasi* Zone (Ludlow).

Yarra Improvement Works (refers to works to straighten the river between the South Yarra Railway Bridge and Princes Bridge, at the end of last century).
*Hapalocrinus victoriae*

NMVP1615, excavation on ridge on W of railway cutting c. 800m WSW of Royal Park Railway Station, Parkville, Melbourne
*Phimocrinus americanus*
*Nassoviocrinus longibrachiatus*
*Trichocrinus morleyi*

Quarry (now in Clifton Park) at West Brunswick between Albert and Victoria Streets.
*Helicocrinus plumosus*

NMVPL2259 in creek bed about 250m N of Heathcote-Nagambie Road, E of Argyle Railway Station, Heathcote (=H41 of Thomas, 1940).
*Clematocrinus argylensis*
*Kroppocrinus heathcotensis*
*Nassoviocrinus corcorani*

NMVPL1925 in creek bed under bridge (on Sunday Creek Road) just west of railway line at Kilmore East.
*Dendrocrinus arrugius*

Upper Yarra (no further details; grouped with other localities having this species).
*Nassoviocrinus longibrachiatus*

Excavation at E end of Melbourne CBD (presumably in area of Spring Street, possibly at Flinders Street intersection; exact locality unknown))
Hapalocrinidae indet.

**Column 1.** Middle *Aegiria thomasi* Zone (Ludlow).

NMVPL1927 at crossing of Broadhurst Creek by Kilmore to Wandong Road (Kilmore Siltstone).
*Dendrocrinus* sp.

# EARLY DEVONIAN ECHINODERMS FROM SOUTH AFRICA

PETER A. JELL AND JOHANNES N. THERON

Jell, P.A. & Theron, J.N., 1999 06 30: Early Devonian echinoderms from South Africa. *Memoirs of the Queensland Museum* **43**(1): 115-199. Brisbane. ISSN 0079-8835.

Echinoderms of the Lower Devonian Bokkeveld Group in the Cape Province, South Africa, have played an important role in sedimentary studies of the region but their taxonomic status has been known from only a few cursory papers. We here provide taxonomic treatment of all available crinoid (15 species), asterozoan (11) and blastoid (2) species revising all previously described taxa and more than doubling the known diversity. Palaeobiogeographic affinities appear to be with Europe and the USA but known faunas of South America and Australia are small and almost certainly incompletely known. New taxa described are the crinoid genera *Mandelacrinus nelsoni*, *Eckidocrinus interbrachiatus*, *Sacrinus gamkaensis*, *S. hexensis*, *Monaldicrinus johni* and *Othozecrinus royi* and the asterozoan genera *Aulacolatiaster breviramus* and *Hotchkissaster macrodentatus*. *Hexuraster* is introduced as a replacement for preoccupied *Hexura* Spencer. New species are the crinoids *Kopficrinus halbichi*, *Cradeocrinus plenarius* and *Thalamocrinus arenaceus* and the asterozoans *Marginura hilleri* and *Eugasterella africana*. ❒ *South Africa, crinoids, starfish, ophiuroids, Early Devonian, Bokkeveld.*

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Echinoderms were first recorded from the Lower Devonian Bokkeveld Group of South Africa as early as 1816 by Dr G. Thom, a clergyman by occupation but also an ardent amateur fossil collector. He gathered 'endless numbers of specimens of shells, trilobites and encrinites or stone lilies' (Thom, 1830). Thus crinoids were the first echinoderms described (Salter, 1856). The Devonian age for the Bokkeveld fossils was assigned about the same time (Sandberger, 1852; Sharpe & Salter, 1856) but in the second half of the 19th century very little was attempted on the identification of these fossils. Rogers and Schwarz mapped these rocks in detail beginning in 1895 and assembled extensive fossil collections that formed the subject of numerous studies illuminating the fossil distribution and stratigraphical setting. Their Devonian age was also confirmed by comparison with faunas from South America and Europe (Corstorphine, 1897; Schwarz, 1906; Reed, 1904, 1906; Knod, 1908; Clarke, 1913; Kozlowski, 1923). In a comprehensive review of the Bokkeveld fauna, Reed (1925) recorded the first carpoid, blastoid and starfish. Echinoderms comprise only a minor element in the fauna however, and detailed descriptions of the various echinoderms in several collections have been rare. Ophiuroids have been mentioned by Rossouw (1933), Spencer (1930, 1950a) and Rilett (1971). Rennie (1936) described carpoids from Gamkapoort, Breimer & Macurda (1972) described blastoids from the Ceres/De Doorns area and Ruta & Theron (1997) described carpoids in detail. In this paper we have revised the description and in many cases the assignment of previously described echinoderms (crinoids, blastoids and asterozoans) and have described substantial new collections from the South African Museum, the Geological Survey of South Africa (mainly collected by J.N.T. during stratigraphic field mapping during the 1970s to 1990s) and the private collection of Mr Roy Oosthuizen of Klaarstroom.

## STRATIGRAPHIC SETTING

The clastic Cape Supergroup borders the southern and western parts of South Africa for 800km eastwards and almost 300km northwards from Cape Town (Fig. 1). The Supergroup is divided into a lower, predominantly arenitic Table Mountain Group, conformably overlain by the markedly argillaceous Bokkeveld Group, which in turn is overlain by the more arenitic Witteberg Group (Fig. 2).

The Bokkeveld Group consists of a cyclical alternation of predominantly argillaceous and arenaceous units. Each of these extensive lithostratigraphic units is given formation status (Fig. 2). The 6 lower formations which can be traced

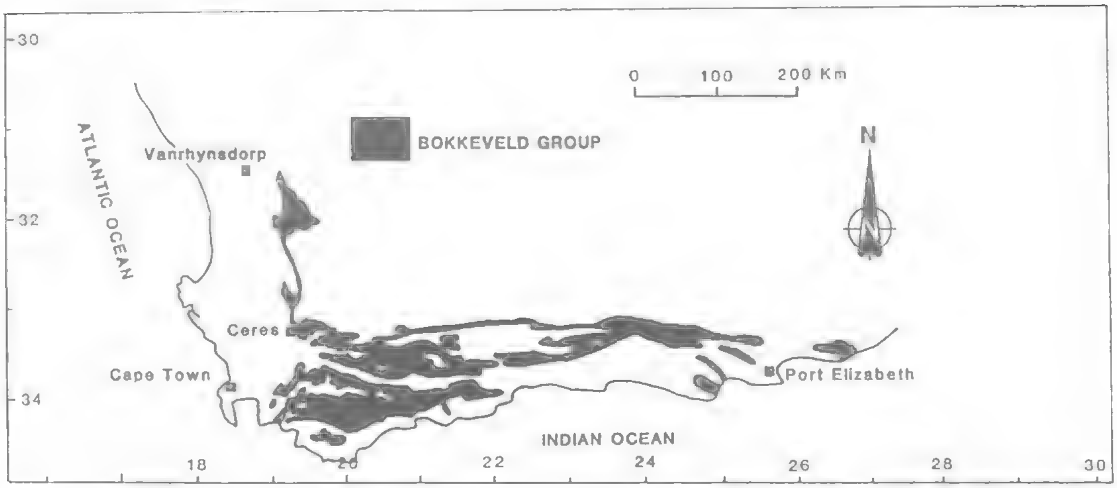



FIG. 1. Sketch map of South Africa showing outcrop areas of the Bokkeveld Group in solid black.

throughout the outcrop area are collectively referred to as the Ceres Subgroup. The upper part of the sequence in the west, with 5 formations, is designated the Bidouw Subgroup, whilst eastwards the laterally equivalent Taka Subgroup consists of 3 formations (Theron, 1972; Theron & Johnson, 1991). Thickness of the Bokkeveld Group is much greater in the east than in the west.

These alternating lithostratigraphic units represent 5 major, sheet-like, superimposed, coarsening-upward cycles which feather out southwards into a relatively homogeneous mudstone-siltstone sequence. This southward decrease of coarser clastics is linked to a progressive thickening of the argillaceous units and of the Bokkeveld Group. The arenaceous units vary from fine-grained quartz arenites to immature arkosic arenites, either horizontally laminated or planar to trough cross-bedded. Hummocky cross stratification becomes a prominent structure northwards (Theron et al., 1995). The argillaceous units consist of dark grey shale, mudstone and siltstone with thin intercalated lenses of fine to medium grained lithic sandstone. The latter reveal swaley cross-stratification and often marked ripple cross laminated zones towards the north.

Weathering of the sequence gives rise to hogback topography, the more resistant arenites creating ridges whereas the intervening argillites generally weather predominantly recessively. This distinctive weathering minimises good exposures of the argillites.

Although numerous fossils have been collected and described, little attention has been paid to their stratigraphic occurrence so that for many years there was no clarity as to whether any zonal scheme could be developed. The faunas vary at a gross level with geography (Schwarz, 1906; Theron, 1972; Oosthuizen, 1984) in that brachiopods and echinoderms are more common in the west, with conulariids, corals and hyoliths more prevalent towards the east.

Usually, marine invertebrate faunas are most common in the Ceres Subgroup, but are found up to the level of the Karoopoort Formation in the west and the Karies Formation in the east (Fig. 2). Although present throughout the Bokkeveld Group, plant and especially trace fossils, become abundant in the northwestern outcrop areas. A wide variety of typically shallow marine ichnogenera occur with large numbers of a variety of the uncommon pentameral stellate trace fossil *Asteriacites* (Fig. 3) at various horizons within these proximal arenites (Theron, 1972).

Examination of sediment/phyla associations reveals distinct affinities of certain species for a particular lithology (Reed, 1907; Theron, 1972; Oosthuizen, 1984). Since a large percentage of the Bokkeveld fauna is benthic organisms, they are likely to be facies controlled. Trilobites and cephalopods tend to occur mainly in argillaceous horizons in contrast to the gastropods, bivalves, and brachiopods which are found more evenly in arenites and argillites. Among echinoderms, the crinoids are found in a variety of sediment types from mudstones to lithic arenites. Although stem fragments are prolific, well-preserved crowns are largely confined to finer grained sediments. Although scarce, ophiuroids, carpoids and

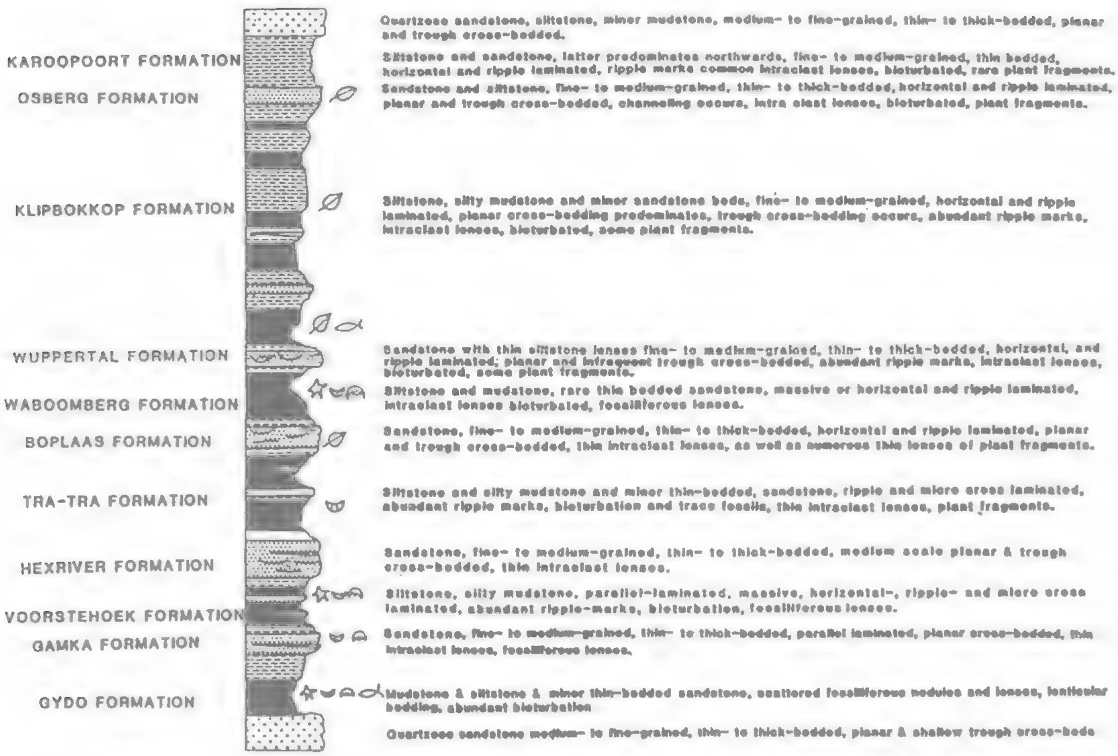



FIG. 2. Stratigraphic section of South African Devonian. The coarse sandstones at top and bottom of section are contiguous parts of the Witteberg (C3) and Table Mountain (C1) Groups, respectively and indicate upper and lower margins of the Bokkeveld Group (C2). All sediments are siliciclastics; solid black = mudstone, horizontal dashes = siltstone and close dots = fine sandstone. Fossil content is indicated by: star = echinoderms; convex down symbol = shells; convex up symbol = trilobites; two curved lines crossing towards righthand end = fish; leaf shaped symbol = plant fragments. A shorthand nomenclature to reflect cyclicity within the Bokkeveld Group has emerged so that the shales (S) alternate with the sandstones (Q)and are numbered from the base up; thus the Gydo Formation is C2S1, the Gamka Formation is C2Q1, the Voorstehoek Formation is C2S2, etc.

blastoids are similarly found mainly in mudstones, shales or silty shales.

Faunal community structures are recognised (Boucot, 1971; Hiller & Theron, 1988). The overall decrease of Bokkeveld invertebrates and increase in plant fragments and ichnofossils to the north as the argillaceous units become sandier, suggests a shallowing of the basin in that direction. There is a corresponding decrease in fossil content in a southerly direction approaching the deep basin (Theron, 1970, 1972; Theron & Loock, 1988).

## PALAEOGEOGRAPHICAL SETTING

The conspicuous change from a few thousand metres of supermature sand (Table Mountain Group) to the predominantly muddy sediments of the Bokkeveld Group throughout the Cape Basin in the Early Devonian, is interpreted as an overall northward advance of the shoreline and progression of shelf and delta slope sediments (Gydo Formation) across the sand-shoal Rietvlei Formation. The latter constituting the uppermost unit of the Table Mountain Group, was deposited in a wide shallow embayment open to the southeast and flanked by a mature low gradient coastal plain (Rust, 1973).

The Bokkeveld sequence reflects the most dynamic phase of the Cape Basin development, when, at the Pragian-Emsian transition, tectonic activity and accelerated downwarping evolved. Pulsatory cyclicity in the vertical stacking of the upward coarsening sequences implies tectonically controlled regressions and transgressions (Theron, 1972; Tankard & Barwis, 1982). These major cycles represent the progradation of lobate wave-dominated deltas along a coastline of moderately high marine energy (Tankard &

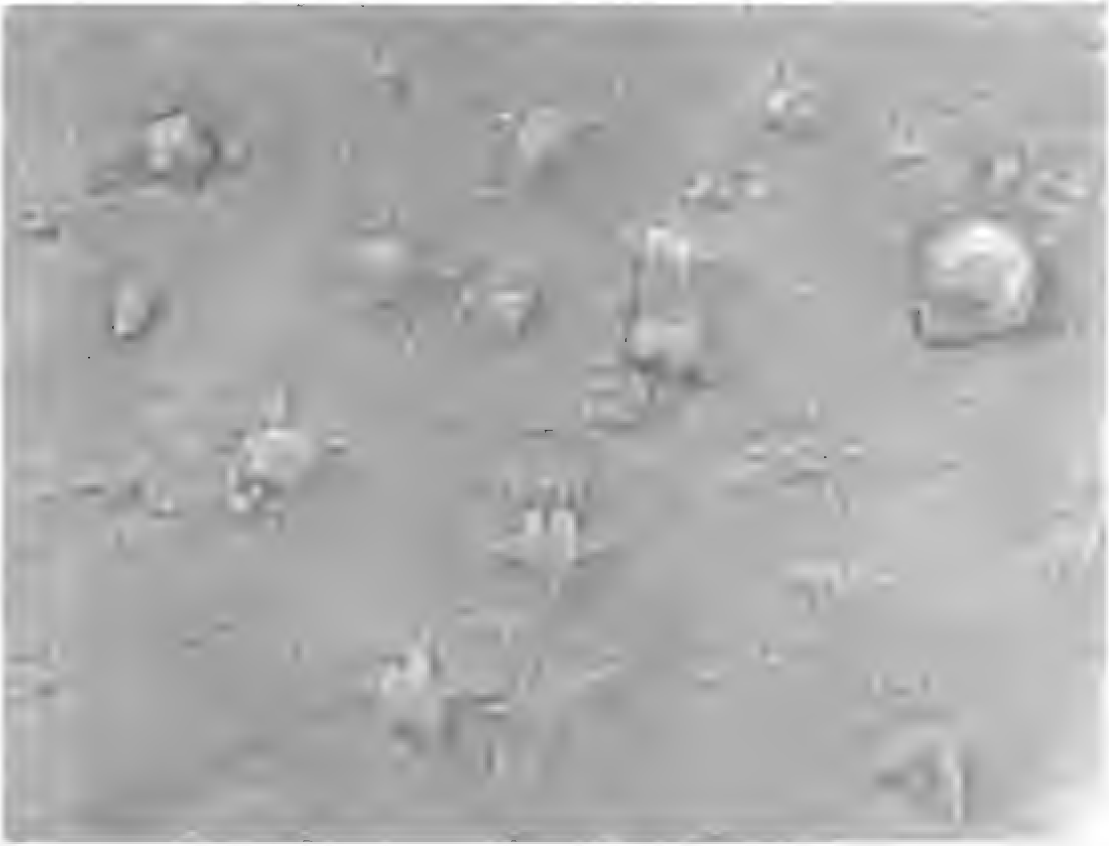


FIG. 3. *Asteriacites* sp. A, assemblage of 10 or more complete or partial individual traces in close proximity. T1451 from Vanrhynsdorp (C2S2), x1.2. (Photo courtesy of John Almond).

Barwis, 1982; Theron & Loock, 1988). Nearshore deposits grade southward into thick shelf mudstones, with the greater thickness towards the eastern Cape reflecting increased downwarping in that direction.

An idealised Bokkeveld genetic sequence consists of sediments laid down successively in the shelf, delta slope and delta platform environments during the constructional phase of delta growth. This is in turn overlain by nearshore marine reworked deltaic deposits, which represent the sediments that evolved during the destructional phase of delta development (Tankard & Barwis, 1982). Storm activity is well-documented in the delta platform sediments, which represent the distributary mouth bar, interdistributary bay and tidal flat deposits, especially in the northern Bokkeveld facies (Theron et al., 1995). Fossils are generally sparse in these sand-, silt-, and mudstones, but occasionally occur as relatively thick lenticular coquinites. Fossils are also generally sparse in the reworked sands of the delta platform. Wave and tidal activity created interspersed barrier washover sheets and tidal inlet and channel fill sequences that were not very conducive to the preservation of fossils.

On the other hand the dark grey mud and siltstones of the Bokkeveld Group contain a rich invertebrate fauna, especially brachiopods and bivalves, which are preserved as scattered internal and external moulds. Coquinites, where present, are relatively thin but laterally persistent; as water depth increased coquinites became rarer. Ebbing storm surge currents entrained shells and sediment from the seafloor and carried them seawards, to where hollows and storm-generated channels acted as traps in which shells and disarticulated crinoidal material accumulated (Hiller & Theron, 1988).

Generally, post-mortem transport of fossils was limited as indicated by the minimal

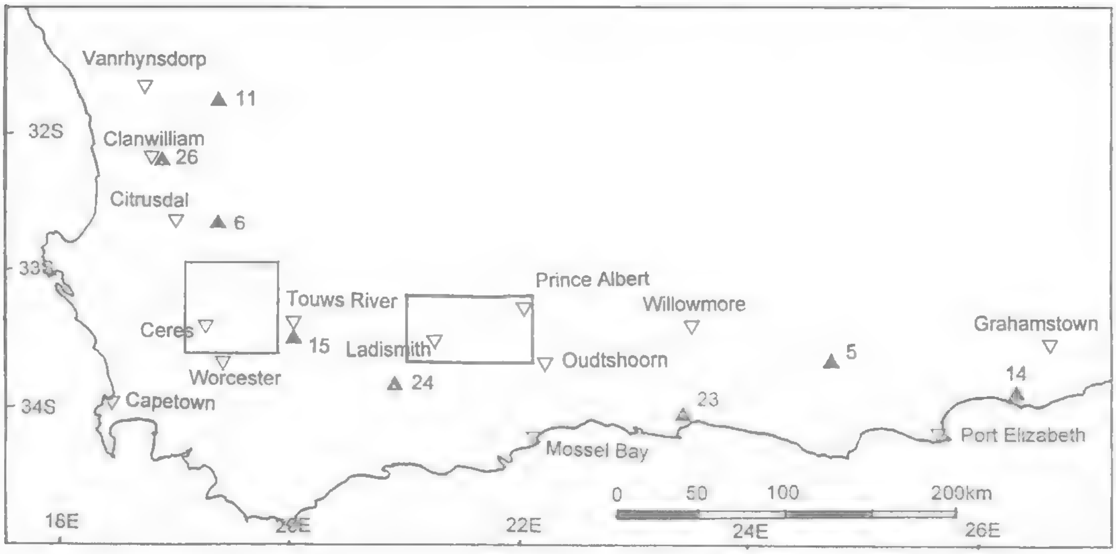



FIG. 4. Sketch map of South Africa indicating the localities from which Lower Devonian echinoderms are known. The 2 frames around the Ceres and Ladismith-Prince Albert districts are enlarged in Figs 5 and 6, respectively. Key to numbered localities outside the frames: 5 = Bucklands; 6 = Grootrivierhoogte; 11 = Platfontein; 14 – Kaaba/Alexandria; 15 = Nouga/Vredefort; 23 = Keurboomstrand; 24 = Warmwaterberg; 26 = Clanwilliam.

mechanical damage to shells. Disarticulated shells are common but rarely display evidence of abrasion or breakage. Furthermore the vulnerability of the multiplated echinoderm skeletons to post-mortem disaggregation generally make preservation of whole crowns relatively rare. In the Gydo and Waboomberg Formations preservation of echinoderms still in life position, indicates predominantly gentle currents and sudden burial, perhaps by smothering mud clouds. Sudden influxes of fine sediment may have come either from the rivers feeding the deltas, or as a result of a storm generating a blanket of wave-stirred mud (Theron, 1972; Hiller & Theron, 1988). This environmental scenario is supported by high concentrations of brittle stars (adult as well as immature individuals), constituting lenticular 'starfish beds' in the Waboomberg mudstones in association with large numbers of infaunal bivalves preserved at a high angle to bedding with their umbones pointing upwards. Co-occurring fenestellid bryozoans, all with the apices of their cones directed upwards suggest overturning by gentle currents. In locally overlying beds well-preserved carpoids are associated with an ostracod fauna and with exquisitely preserved *Lingula,* which are not in life position (Ruta & Theron, 1997; Becker et al., 1994). The frequency of asterozoan trace fossils in the northern proximal shallow marine beds substantiate the original abundance of starfish and brittle stars in the marginal Bokkeveld seas. The relative rarity of asterozoan body fossils in the Bokkeveld sequence is therefore a reflection of the disintegration of their complex skeletons after death. Both ophiuroids and asteroids probably constituted quite an important component of the normal prevalent benthic marine biota of the Bokkeveld Group.

Available data allow correlation (Boucot, 1971; Hiller & Theron, 1988) of several benthic invertebrate fossil communities with various depositional subenvironments in a delta complex: 1, a tidal flat community dominated by inarticulate brachiopods and infaunal bivalves inhabited the sheltered, back-barrier environment; 2, the distributary mouth bar community dominated by brachiopods, occupied the relatively turbulent shallow water setting at the seaward edge of the delta platform; 3, the delta slope community was of intermediate aspect, dominated by brachiopods but more diverse with infaunal bivalves, gastropods, crinoids, cricoconariids and especially trilobites; 4, the shelf community, which although still dominated by brachiopods, is the most diverse community; brachiopods constitute <1/2 the diversity of the assemblage, with trilobites, bivalves and gastropods well represented and echinoderms,

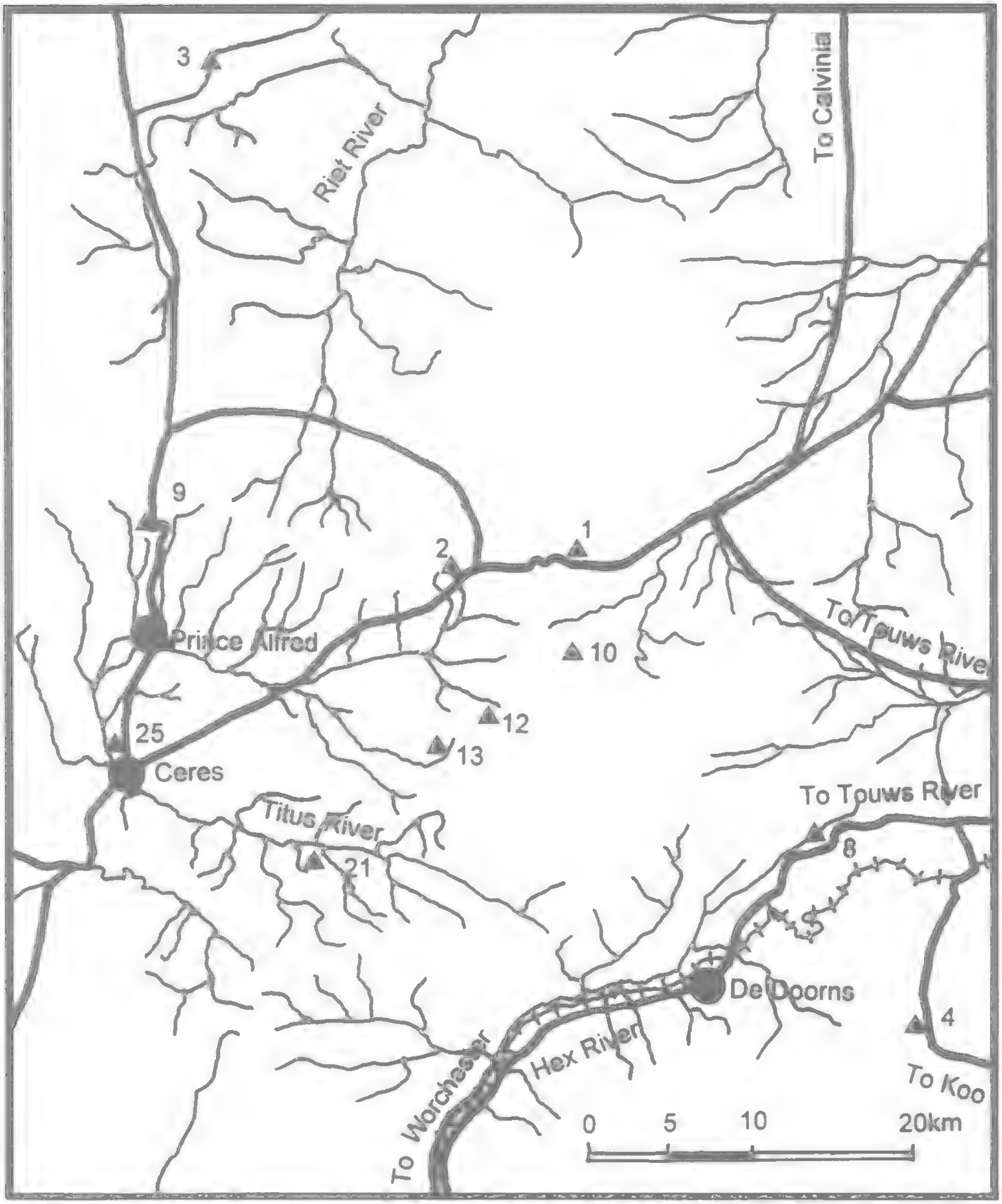



FIG. 5. More detailed locality map of Ceres district as outlined by lefthand frame in Fig. 4. 1=Hottentotskloof; 2=Theronsberg Pass; 3=Tafelberg/Boplaas; 4=Matroosberg/Vredelus; 8=Hex River Pass; 9=Gydo Pass; 10=Die Vlakte; 12=Klipfontein/Lakenvlei; 13=Swaarmoed; 21=Eselfontein; 25=Ceres. Thick black lines are roads; thin crossed line (lower right) is a railway; thin black lines are streams.

hyolithids, corals, bryozoans, conulariids and cephalopods comprising a significant proportion.

In the Gydo and Gamka Formations, which constitute the oldest deltaic cycle, these communities are well-represented. Shelf and

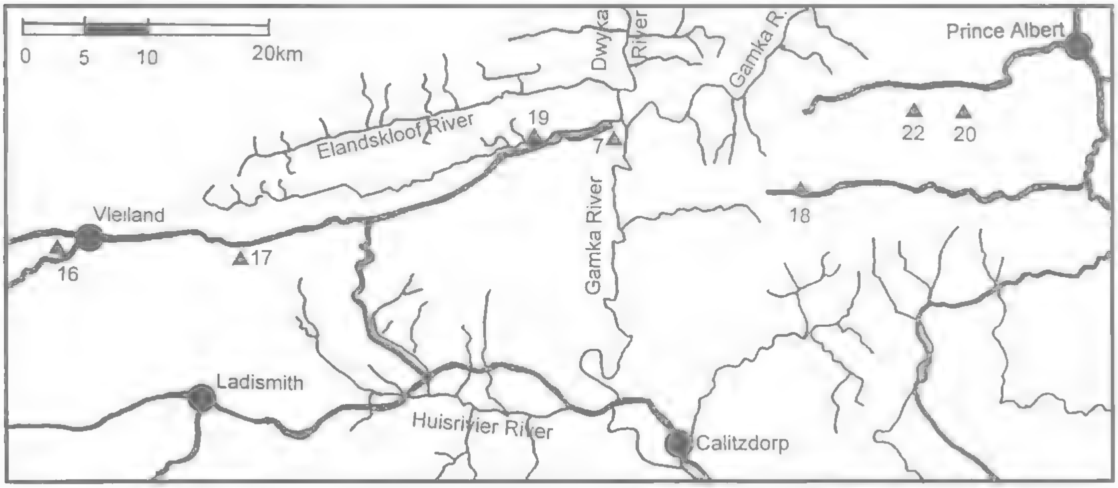



FIG. 6. More detailed locality map of Prince Albert-Ladismith districts as outlined by righthand frame in Fig. 4. 7 = Gamkapoort Dam; 16 = Vleiland; 17 = Koudeveld; 18 = Gamkaskloof; 19 = Bosluiskloof; 20 = Damascus; 22 = Vrischgewaagd. Thick black lines are roads; thin black lines are streams.

slope communities are found in the Voorstehoek Formation and in western outcrops of the Waboomberg Formation, shelf community assemblages have been identified as well. In many of the other formations, available collections are generally too small for community analysis (Hiller & Theron, 1988).

## FAUNAL AFFINITIES

All Bokkeveld echinoderm specimens known to the authors were included in the present study. Affinities of the taxa identified (Table 1) are highly equivocal. One bias in this assessment is the variation in levels of knowledge from other parts of the world. The fauna of North America is the best known and in general, most recently studied; in Europe comparably large faunas are known but many have not been given a modern taxonomic treatment; South America and Australia have faunas of this age but they are poorly known (e.g. Australian crinoids (Jell, 1999) as demonstrated in this volume). Early Devonian echinoderms from other parts of the world are virtually unknown and not able to be compared. At species level the South African fauna has a crinoid and an asterozoan in common

TABLE 1. Faunal affinities of the South African echinoderms dealt with herein compared with Europe (1), North America (2), South America (3) and Australia (4). G = the genus occurs in that continent; cf G = a closely related genus occurs in common; S = the species also occurs in that continent; and F = the family is in common.

| CRINOIDS | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| *Ophiocrinus stangeri* Salter, 1856 | | G | | G |
| *Ophiocrinus* sp. cf mariae (Kier, 1952) | | cf S | | G |
| *Corocrinus imbecillus* Schmidt, 1941 | S | G | | |
| *Mandelacrinus nelsoni* gen. et sp. nov. | cf G | cf G | | |
| Monocyclic camerate indet. | | cf G | | |
| *Arthroacantha*? sp. | | ?G | | |
| *Eckidocrinus interbrachiatus* gen. et sp. nov. | | | | |
| *Kopficrinus halbichi* sp. nov | | G | | |
| *Monaldicrinus johni* gen. et sp. nov | cf G | cf G | | |
| *Sacrinus gamkaensis* gen. et sp. nov | cf G | | | |
| *Sacrinus hexensis* gen. et sp. nov | cf G | | | |
| *Cradeocrinus plenarius* sp. nov | G | G | | |
| *Thalamocrinus arenaceus* sp. nov. | | G | | |
| *Othozecrinus royi* gen. et sp. nov | | cf G | | |
| ASTEROZOANS | | | | |
| *Aulacolatiaster breviramus* gen. et sp. nov. | cf G | cf G | | |
| *Ulrichaster macrodentus* gen. et sp. nov | G | G | | |
| *Haughtonaster reedi* Rilett, 1971 | | cf G | cf G | |
| *Hexuraster weitzi* (Spencer, 1950a) | F | F | | F |
| *Encrinaster tischbeinianus* (Roemer, 1862) | S | | | |
| *Marginura hilleri* sp. nov. | | | G | |
| *Eugasterella africana* sp. nov. | | G | | |
| *Strataster ohioensis* Kesling & LeVasseur, 1971 | | S | | |
| *Strataster stuckenbergi* (Rilett, 1971) | | G | | |
| BLASTOIDS | | | | |
| *Pachyblastus dicki* Breimer & Macurda, 1972 | | | S | |
| *Brachyschisma ootheizeni* Breimer & Macurda, 1972 | | G | | |

with Europe, a crinoid and an asterozoan with North America and a blastoid in common with South America. At the generic level most matches are with North America, then Europe, then a very few with South America and Australia. The 25 South African echinoderms dealt with herein do not provide a statistically large enough sample to make any compelling arguments and thus the affinities must be considered unknown at this stage. Brachiopod affinities (Boucot et al., 1969) place South Africa in the cool water Malvinokaffric Realm suggesting that further study of South American echinoderms may reveal closer affinities.

## SYSTEMATIC PALAEONTOLOGY

The following abbreviations indicate repositories for the material discussed in the text:- British Museum of Natural History (BMNH), Geological Survey of South Africa, Pretoria (PRV), Geological Survey of South Africa, Bellville in Capetown (B), Roy Oosthuizen Collection, Zwartskraal, Prince Albert (RO), South African Museum, Capetown (SAM), Geological Collections, Stellenbosch University, South Africa (SU), Rhodes University, Grahamstown (RUGDNH), Natal Museum, Durban (NM) and Sedgwick Museum, Cambridge University, England (SM A). All illustrations are of latex casts taken from external moulds unless otherwise stated; they are whitened with a sublimate of ammonium chloride for photography.

### Class CRINOIDEA Miller, 1821

Terminology follows Moore & Teichert (1978). Measurements are given as: length, parallel to the central axis; width, transverse to, but never cutting or joining the central axis; and depth, normal to, and may join central axis.

### Subclass CAMERATA Wachsmuth & Springer, 1881
### Order DIPLOBATHRIDA Moore & Laudon, 1943
### Superfamily RHODOCRINITOIDEA Roemer, 1855
### Family OPSIOCRINIDAE Kier,1952

Although Kier (1958) advocated elimination of the Opsiocrinidae after he recognised that *Opsiocrinus* was dicyclic, Ausich (1986) found the family useful in his classification of the Rhodocrinitoidea. Frest & Strimple (1981) and Ausich (1986) recognised that several of his familial characters are of generic standing in some cases in the same group. With this in mind the classification may be considered preliminary. Frest & Strimple (1981) and Ausich (1986) recognised the cofamilial relationship of *Opsiocrinus* and *Ophiocrinus*; we consider these genera synonyms (see below). We use Ausich's (1986) classification herein but following ICZN Article 40 the family name based on the junior synonym remains valid.

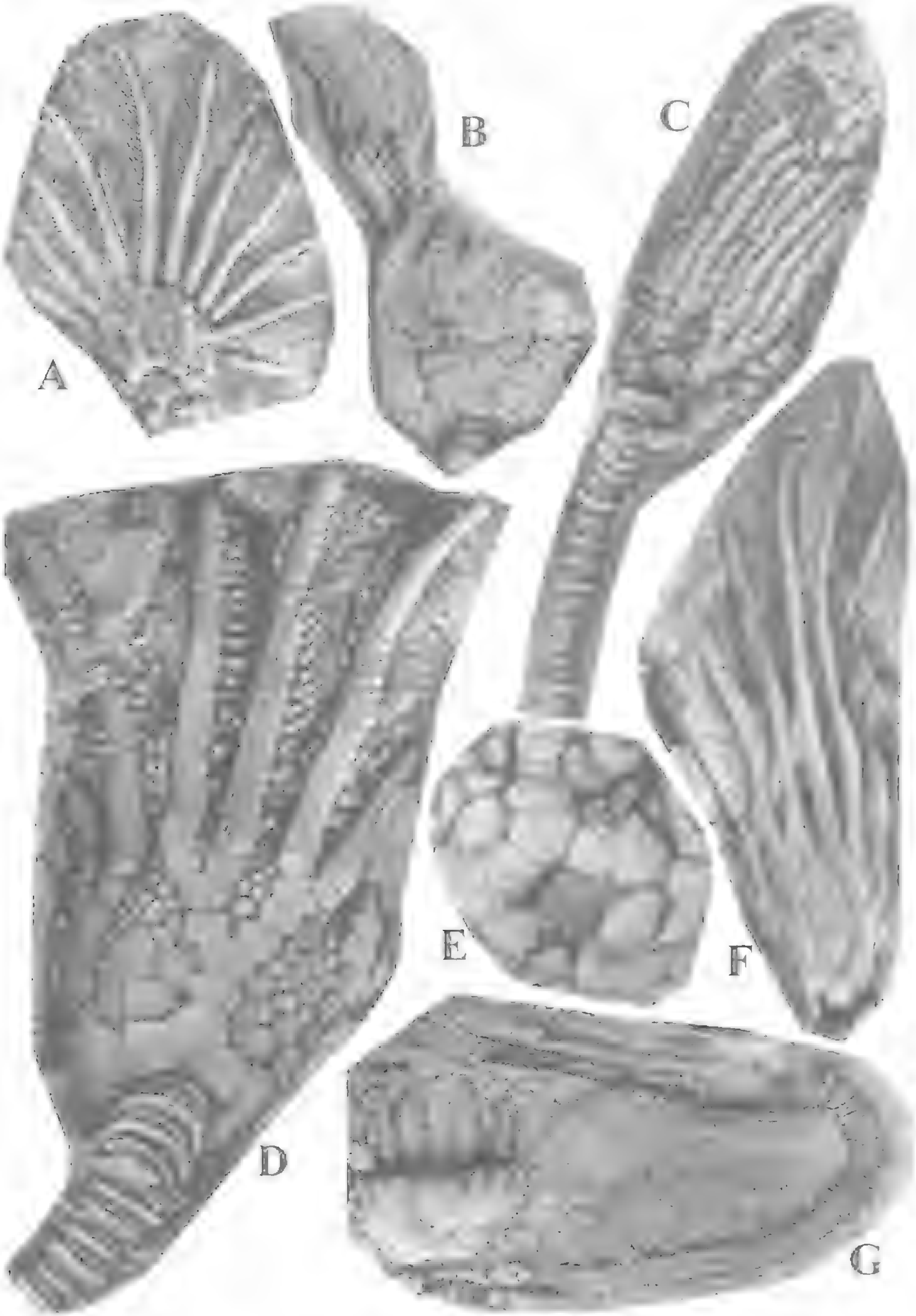
### **Ophiocrinus** Salter, 1856

TYPE SPECIES. *Ophiocrinus stangeri* Salter, 1856 from the Lower Devonian Bokkeveld Series, South Africa; by monotypy.

DIAGNOSIS. Infrabasals 5, forming a pentagon completely or almost completely concealed by stem; interbrachials numerous, depressed, small, regular, especially in proximal part of interrays; CD interray conspicuous, with anitaxis of subquadrate anal plates variously developed in field of small irregular plates on either side. Arms 10 or 20, free and becoming cuneate then biserial distal to last arm division, unbranched distally. Stem circular or pentagonal in section, with narrow marginal crenularium, heteromorphic.

REMARKS. The only significant differences between *Opsiocrinus* Kier,1952 and *Ophiocrinus* appear to be the number of arms, length of anitaxis and cross section of the stem. Frest & Strimple (1981, table 1) showed that the2 genera

FIG. 7. *Ophiocrinus stangeri* Salter, 1856. A, deformed crown with pinnulate biserial arms, RO39, ×1. B, C-D interray view of crown showing 3 vertical columns of anal plates B4603, ×2. C, small specimen showing uniserial arms well away from theca and biserial arm on left high up, B4544, ×3. D, holotype crown with C-D interray on left, with 1st interprimibrach supporting 4 anal plates, with uniserial brachials proximally gradually becoming cuneate then biserial distally, SM A3441, ×4. E, basal view of small cup showing subpentagonal stem facet, from the Gydo Formation in a quarry on E side of road N from Prince Alfred's Hamlet, 1km S of Gydo, B4670, ×5. F, small deformed crown SAM13479, ×2. G, two crowns compressed in the same direction, that on left with diminished crown length and that on right compressed laterally and showing the infrabasal circlet on top of the stem viewed from inside the cup, SAMK972, ×1.25.


A
B
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are distinguished only by the number of arms and in the nature of arm brachials. Although there is a reversal (clearly a typographical error) between their text and table 1 with *Ophiocrinus* being credited with cuneate brachials in the text but biserial ones in table 1. Regardless of this confusion the larger collection of *O. stangeri*, now available, allows confirmation that the arms in both genera progress distally from rectangular to cuneate to biserial. Length of the anitaxis, with 4 plates in one genus and 2 in the other could well be considered a specific discriminator if consistent (1 CD interray is available for *Ophiocrinus* and 2 for *Opsiocrinus*). Some camerate genera contain species with different numbers of arms. One specimen of *O. stangeri* (Fig. 2C) has a ray with only 2 arms as opposed to the usual 4 in adjacent rays; a 2nd specimen (Fig. 1B) shows the beginnings of the radial interplate ridge patterns so prominent in some *Opsiocrinus mariae* Kier, 1952 (Kesling & Chilman, 1975, frontispiece, pl.40, figs 11-14); several specimens (Fig. 1A, 2A, 3B) have slight, barely visible re-entrants in the proximal margin of the basal plates which probably accomodated the corners of the infrabasal pentagon as in *O. mariae*. This indicates that orientation of the infrabasal pentagon to the basal circlet changed from the exterior to the interior as described by Kier (1958, fig. 1) in *O. mariae* because the interior of the cup in *O. stangeri* (Fig. 3E) shows the infrabasal pentagon with the angles at the sutures between basals and the sutures between infrabasals at the centre of the basals. The stem of the North American species is inferred to be pentagonal because of the shape of the attachment facet on the cup. In *O. stangeri* the stem is round but in at least 1 specimen (Fig. 1G) the attachment facet or the 1st columnal is pentagonal. Thus we synonymise these 2 genera despite their geographic and stratigraphic (Early Devonian vs Middle Devonian) separations. Ausich (1986:87) inferred 2 lineages within the Opsiocrinidae from the Llandovery into the Devonian with the 2 Devonian genera on separate lineages based on cup shape, prominence of ridges and arm numbers. However, cup shape and ridge pattern are identical in the 2 Devonian genera and taking the rudimentary ridge pattern in a specimen of *Ophiocrinus* even the interbrachial ornament may be allied. The relation of the infrabasal circlet to the basal circlet is another feature which seems to join the 2 Devonian genera. Other monophyletic camerate genera are known to have 10 and 20 armed members and we suggest that *Ophiocrinus* and *Opsiocrinus* constitute 1 genus and belong to 1 lineage rather than 2 that had been separate since the Early Silurian (Jell, 1999, fig. 2).

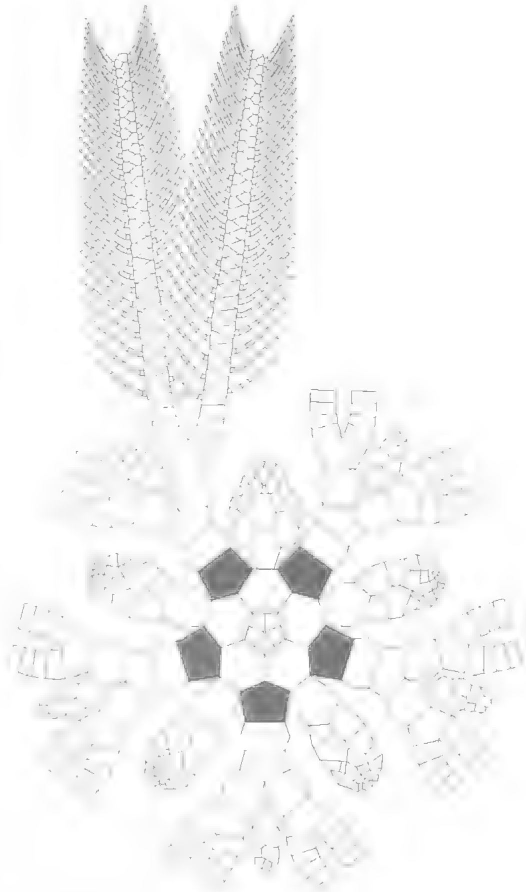


FIG. 8. *Ophiocrinus stangeri* Salter, 1856, plate diagram showing stem facet as dashed circle, radials black and only 2 incomplete arms from half of one ray; posterior interray at 12 o'clock.

**Ophiocrinus stangeri** Salter, 1856
(Figs 7-10)

*Ophiocrinus stangeri* Salter, 1856:223, pl.25, fig.20; Ubaghs, 1978: T428, fig. 238.2.

MATERIAL. HOLOTYPE: SMA3441 from De Dooms, Hex Rivier Poort (donated to the Sedgwick Museum, Cambridge in 1932 from the collection of Dr W. Stanger. B4523 from Bucklands, eastern Cape Province(C2S1), B4526-4530 from Gamkapoort Dam (C2S1), B4544, B4553, B4603 from Gydo Pass (C2S1), B4551, B4552 from Gamkapoort Dam (C2S1), RUGDNH1 from Klein Kaaba, Alexandria district, eastern Cape (Voorstehoek Formation), B4579; RO S17, RO S20 from Grootrivier,


FIG. 9. *Ophiocrinus stangeri* Salter, 1856. A, crown showing B and C rays, RO S20, ×5. B, small crown with arms on anterior (or A ray) side missing to expose anal tube, K4532, ×4. C, large crown showing some normal arms (on right) but mostly arms that have been broken off during life and regenerated producing major change in arm diameter, B4553, ×2.5. D, crown on long stem suggesting high level feeder, SAM13459, ×1.


FIG. 10. *Ophiocrinus stangeri* Salter, 1856. A, small crown showing changing brachial type B4544A, ×5. B, small crown SAMK973, ×2. C, poorly preserved crown from most northerly outcrops in Calvinia district. B4559, ×5. D, crown RO S17, ×2.5. E, interior of crown showing 5 infrabasals. RUGDNH1, ×2.5.

Ceres at 32°38'S, 19°24'15"E (C2S1), RO39 from Gamkapoort at 33° 18'S, 21° 38'E (C2S1), SAMK967, 969, 970, 972, 973, 975 from Wolfaardt's Farm, Riet Valley, Ceres, SAM9703 from Clanwilliam, Cape Province, SAM13459 from Boschluis Kloof, SAM13462, 13464, 13479 from Koudeveld Berg, above 2nd sandstone.

DESCRIPTION. Crown up to 60mm long, subcylindrical, with arms about 3 times as long as cup. Cup bowl-shaped, up to 25mm maximum diameter, of moderate length, with smooth plates. Infrabasals 5, small, equal, diamond-shaped, concealed by stem. Basals 5, 7- sided, longer than wide, with greatest width in proximal 1/2, rarely with depressed and weakly isolated lateral tips beneath tips of radial (e.g., in holotype), often with slight re-entrant in proximal side presumably accomodating angle of the infrabasal pentagon. Radials 5, pentagonal, not in contact with other radials, penetrating deeply into basal circlet; radial facet plenary. First primibrach hexagonal, wider than long; 2nd primibrach axillary, pentagonal; secundibrachs 2 or rarely 3, fixed, subquadrate; tertibrachs free, becoming triangular distally. Arms 20 (rarely 18), uniserial proximally, becoming almost biserial distally, pinnulate with pinnules on long side of triangular tertibrachs alternating from side to side on successive plates, with well-developed oral groove. CD interray with 2 large hexagonal plates forming central anal column flanked by smaller polygonal anal plates; primanal hexagonal, in radial circlet, similar in size to radials. Interprimibrachs small, numerous in each ray; proximal 1 septagonal, resting on basals; 2 in second row, 3 in next row, increasing in number and decreasing in size distally; interbrachial field decreasing in width adjacent to secundibrachs as arms spread laterally. Intersecundibrachs in larger specimens, 1 in first row, 2-3 in more distal rows. Tegmen unknown. Stem circular, heteromorphic, noditaxis N212 proximally with nodals longer and of greater diameter than internodals, distally with noditaxis N3231323, with intercolumnal sutures strongly crenulate, greatest length among available specimens 15cm (uniform diameter of 2mm), greatest diameter 4mm.

REMARKS. Among available specimens only the holotype shows the CD interray so we have no data on possible variation in this area of the cup, nor any data on the tegmen which is concealed by the arms. One specimen (Fig. 9B), here tentatively assigned to *O. stangeri*, has a long anal tube, about 1/2 length of arms and covered by small polygonal plates; the tegmen of this common species should be sought in future collecting to confirm this feature. The unbranched, free, pinnulate arms in which the brachials become more and more cuneate distally together with a fragment of stem identical with that of *O. stangeri* lying beside the cup suggest assignment to *O. stangeri*; negative evidence is provided by the lack of any other species with this type of arm in the rest of the South African Bokkeveld crinoids available at present. We make the assignment tentative in the absence of detail of the cup.

Some intraspecific variation is recorded in the description above with other variation: 1, in a few specimens (Fig. 7C, F) the distal noditaxis extends much further proximally i.e. proximal stem resembles distal stem of most specimens; 2, in some specimens, particularly smaller ones (c.7mm cup diameter) proximal tertibrachs are more quadrate than rectangular in lateral view, becoming cuneate distally; 3, intersecundibrachs are not present in these smaller or even some larger specimens; 4, in one specimen (Fig. 7B) the threeway intersections of sutures in the interprimibrach and intersecundibrach areas are depressed, suggesting a subtle interplate ridge system as in *Opsiocrinus*.

At species level this taxon is unmistakeable and distinct from the most similar *O. mariae* Kier,1952 in number of arms, depression and ornament in interbrachial areas and CD interray plating. *O. stangeri* is the most common crinoid in available collections from the Bokkeveld Series but is still incompletely known.

**Ophiocrinus** sp. cf. **mariae** Kier, 1952
(Fig. 11)

MATERIAL. A cup RO179 from Cockscomb Mountains, Steytlerville, near Bucklands at 33°31'S, 24°44'30"E in the Gydo Formation.

DESCRIPTION. Infrabasal circlet just visible laterally, with sutures between infrabasals directed at midline of basals, angles of infrabasals directed at sutures between basals; strong ray ridges elevated, occupying most of plate width from basals up to at least 2nd secundibrach; 10 arms; interprimibrach series 1-2-3 decreasing in size at level of arm branch, with strong radial ornament of central tubercle and radial lines sometimes consisting of a series of tubercles, with 7 radial ridges on the 1st interprimibrach, with 6 ridges on plates of next row; 1-2 intersecundibrachs with 5-rayed ornament.

REMARKS. This specimen may represent an undescribed species but it resembles *O. mariae* Kier,1952 more than it does the South African *O.*

FIG. 11. *Ophiocrinus* sp. cf. *O. mariae* (Kier,1952) partial cup showing depressed interbrachials with stellate ornament, RO179, ×5.

*stangeri*: its 10 arms, 2nd primibrach axillary, strongly depressed interbrachial plates with stellate ornament, and strongly depressed 3-way sutural junctions in the cup are features of *O. mariae* but the laterally visible infrabasals, ray ridges standing high on the arm plates and 7-rayed ornament on the 1st interprimibrach differ from that species. It is simply distinguished from *O. stangeri* by its 10 rather than 20 arms and the ornament on the interprimibrachs. Without knowledge of the posterior, stem or higher arms we prefer to make tentative assignment only.

Order MONOBATHRIDA
Moore & Laudon,1943
Suborder COMPSOCRININA Ubaghs,1978
Superfamily PERIECHOCRINOIDEA
Bronn,1849
Family PERIECHOCRINIDAE Bronn,1849

**Corocrinus** Goldring,1923.

TYPE SPECIES. *Corocrinus ornatus* Goldring,1923 from the Middle Devonian Ludlowville Shale, New York; by original designation.

**Corocrinus imbecillus** Schmidt,1941
(Figs 12)

*Corocrinus imbecillus* Schmidt, 1941: 97, pl. 14, figs 3,4.

MATERIAL. HOLOTYPE: E3142 in the Museum für Naturkunde, Berlin, from the Lower Devonian, Upper Koblenz Shale, western Germany. South African material ROC25, ROT17 and B4551 all from Gamkapoort Dam in the Gydo Formation.

DIAGNOSIS. Like type species but with 20 arms.

DESCRIPTION. Cup high conical, up to 20mm maximum diameter, of moderate height; plates with strong radial ornament, with high ray ridges; ray ridges wide on basals, becoming higher relative to the plates and more narrowly arched in section above the axillary primibrach. Basals 3, sutures in B and E rays and CD interray, equal, pentagonal, visible in lateral view, with 3 prominent ridges radiating distally. Radials 5, hexagonal (A,C,D) or heptagonal (B,E), in contact with other radials except in CD interray, slightly longer than wide, with 6 strong radial ridges including ray ridge. First primibrach hexagonal, longer than wide, with 6 radial ridges; 2nd primibrach axillary, pentagonal, with 5 radiating ridges including the Y-shaped ray ridge. Secundibrachs elongate, fixed, with 2nd or 3rd axillary, (most often both axillary in 1 arm but any pattern not available). Tertibrachs free, uniserial, with interbrachial sutures becoming oblique distal to 2nd or 3rd brachial but brachials never triangular. Arms 20, uniserial, strongly pinnulate; pinnules long (up to 1cm long in available specimens), of 8 or more pinnulars, 1 per brachial, alternating from side to side up arm. CD interray wide, with ridge up median line of plates (Fig. 12A); primanal large, heptagonal, in radial circlet, similar in size to radials, supporting 3 hexagonal anals distally. Interprimibrach series elongate, with proximal one hexagonal, resting on 2 radials, supporting 2 smaller hexagonal interprimibrachs in next row, all with 6 radial ridges; more distal rows of smaller plates with central tubercules and radial ridges. Intersecundibrachs numerous, 1 in proximal row, small, centrally tuberculate. Anal sac (Fig. 12C) of many small polygonal abutting plates, about as long as cup, possibly flexible. Stem circular, heteromorphic, with noditaxis of N212 pattern; intercolumnal sutures strongly crenulate; greatest length among available specimens 90mm, diameter 3mm proximally, 2mm distally.

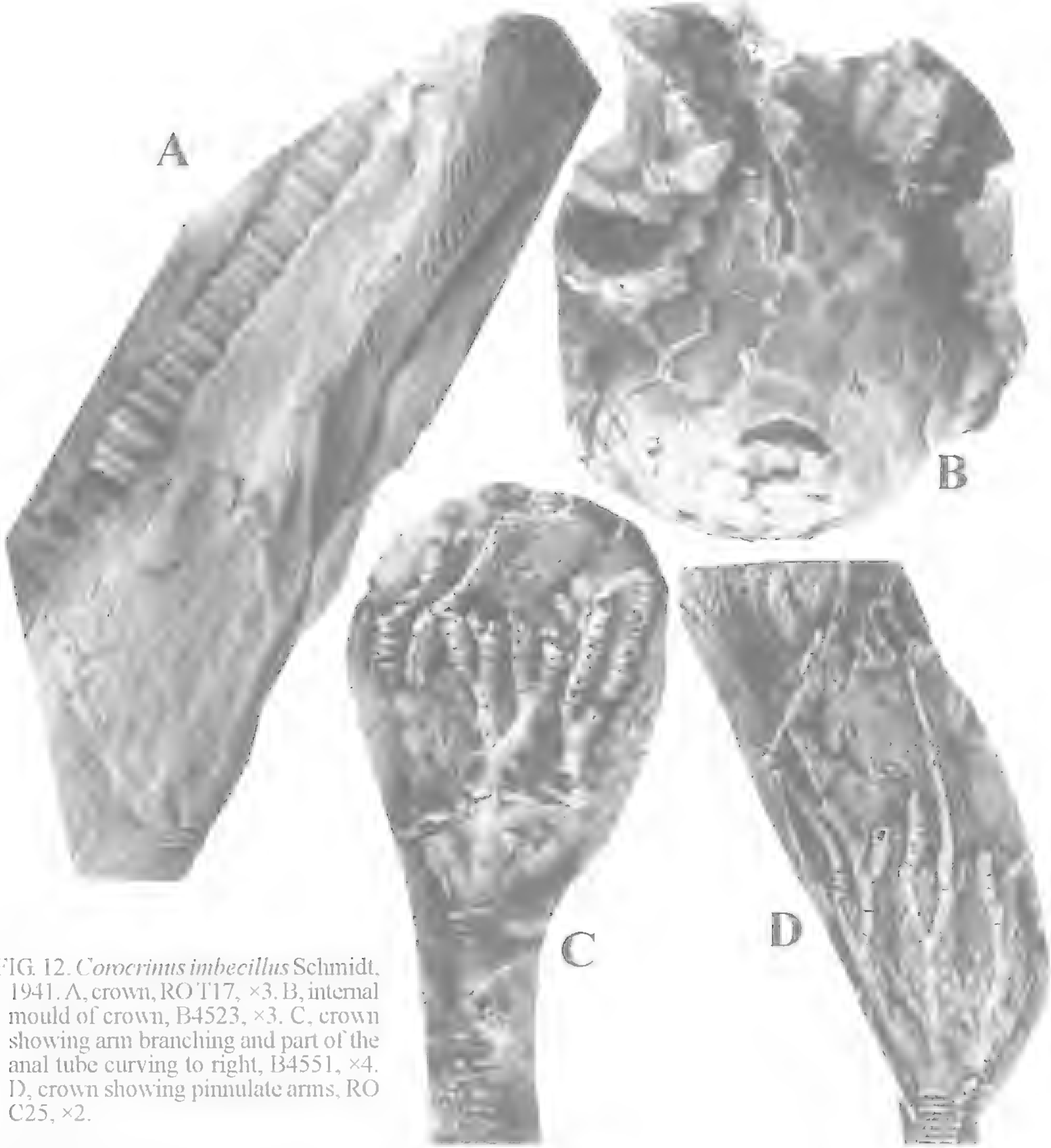



FIG. 12. *Corocrinus imbecillus* Schmidt, 1941. A, crown, RO T17, ×3. B, internal mould of crown, B4523, ×3. C, crown showing arm branching and part of the anal tube curving to right, B4551, ×4. D, crown showing pinnulate arms, RO C25, ×2.

REMARKS. Breimer (1962) noted the close similarity of this species to the type species and we can only make species distinction on the number of arms; none of Goldring's (1923) material of the type species has any free arms attached so that if a further bifurcation occurred in the free arms it would not be available on her material. We therefore, reserve the possibility that *C. ornatus* and *C. imbecillus* could be synonymous. Breimer (1962) placed weight on the axillary primibrach having 7 sides; externally the axillary primibrach of *C. imbecillus* is not clear on Schmidt's (1941) material or on the South African specimens but the internal mould (Fig. 12B) shows the shape of cup plates very well and the axillary primibrach is 7-sided, agreeing with Ubaghs diagnosis.

**Mandelacrinus** gen. nov.

TYPE SPECIES. *Mandelacrinus nelsoni* sp. nov.

ETYMOLOGY. For Nelson Mandela, President of South Africa.

DIAGNOSIS. Cup low conical; plates smooth, with margins depressed in interadii, with strong wide ray ridges leaving narrow depressed marginal zone on fixed brachials. Basals 3, sutures in B ray, CD interray (and presumably E ray). Radials hexagonal, laterally in contact except in CD interray. First primibrach hexagonal; 2nd primibrach axillary, pentagonal. CD interrary wider than other interrays, primanal interrupting radial circlet, supporting 3 hexagonal anals in 2nd row, 5 in 3rd row, 6 in 4th row at level of 1st secundibrach then diminishing on to tegmen. Interprimibrachs small with central tubercle distal from 3rd row. Intersecundibrachs small, tuberculate. Arms 20, biserial distal to 2nd tertibrach, pinnulate; pinnules long, slender, a row along either side of arm, 1 per brachial. Stem circular, of alternating nodals and internodals proximally.

REMARKS. Three basals, separation of C and D radials by the primanal, other radials in contact and hexagonal 1st primibrach suggest the Periechocrinidae but the single fixed secundibrach is not a feature of that family. However, co-familial *Corocrinus* has only a few fixed secundibrachs and makes a reasonable ancestor for the new genus. The shorter cup, wider interradii, less ornamented cup, biserial arms and single fixed secundibrach may all be considered derived character states relative to *Corocrinus*.

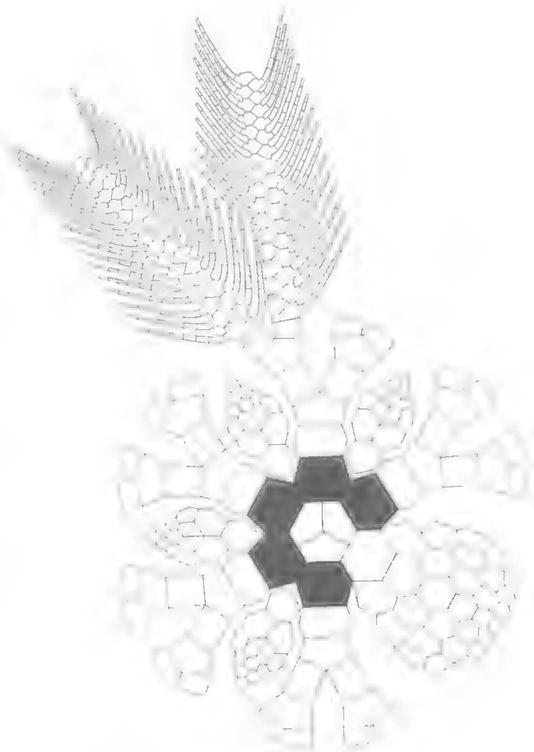


FIG. 13. *Mandelacrinus nelsoni* gen. et sp. nov., sketch of plate arrangement with radials darkened; anterior - posterior axis in NW-SE line; most arms shown as far distally as 1st tertibrachs with distal portions (not including tips) sketched for 2 arms on left of B ray.

**Mandelacrinus nelsoni** sp. nov.
(Fig. 13, 14)

MATERIAL. HOLOTYPE: RO740 from the Cockscomb Mountains, Steytlerville, near Bucklands at 33°31'S, 24°44'30"E in the Gydo Formation. PARATYPE: SAMK976 from Wolfaardt's Farm, Riet Valley, Ceres..

DIAGNOSIS. As for genus.

DESCRIPTION. Cup 6-13mm long, low conical, up to 15mm diameter; plates smooth, with depressed margins, with well-developed ray ridges standing well above lateral parts of plates particularly about the secundibrach level where arms begin to stand away from cup. Basals 3, sutures in B and E rays and CD interray, equal, pentagonal, visible in lateral view. Radials 5, hexagonal, in contact with other radials except in CD interray, wider than long in holotype, longer than wide in small specimen. First primibrach hexagonal, wider than long; 2nd primibrach axillary, pentagonal; 1st secundibrach fixed, hexagonal, with flat lateral areas rising up strongly to high ray ridge; 2nd secundibrach axillary, pentagonal; tertibrachs free, biserial from 2nd. Arms 20, biserial from 2nd tertibrach, strongly pinnulate; pinnules long (up to 1cm long in smaller specimen), of 7-8 pinnulars, 1 per 1/2 brachial in 2 rows along arm. CD interray wide, with ridge up median line of plates (Fig. 6B); primanal large, heptagonal, in radial circlet, similar in size to radials, supporting 3 hexagonal anals distally, followed by rows of 5 then 6 anal plates, then decreasing in size and number between maximum width of fixed arms. Interprimibrach series narrow, elongate; 1st interprimibrach hexagonal, resting on 2 radials, supporting 2 large hexagonal interprimibrachs distally; 3rd row of 3 small centrally tuberculate plates and 4th row same but with 5 plates. Intersecundibrachs 1 or 3, 1 in proximal row, centrally tuberculate, 2 in distal row. Tegmen unknown. Stem circular, up to 4mm in diameter, heteromorphic proximally becoming uniform distally, noditaxis uncertain but probably N212; intercolumnal sutures strongly crenulate; greatest length available 3cm.

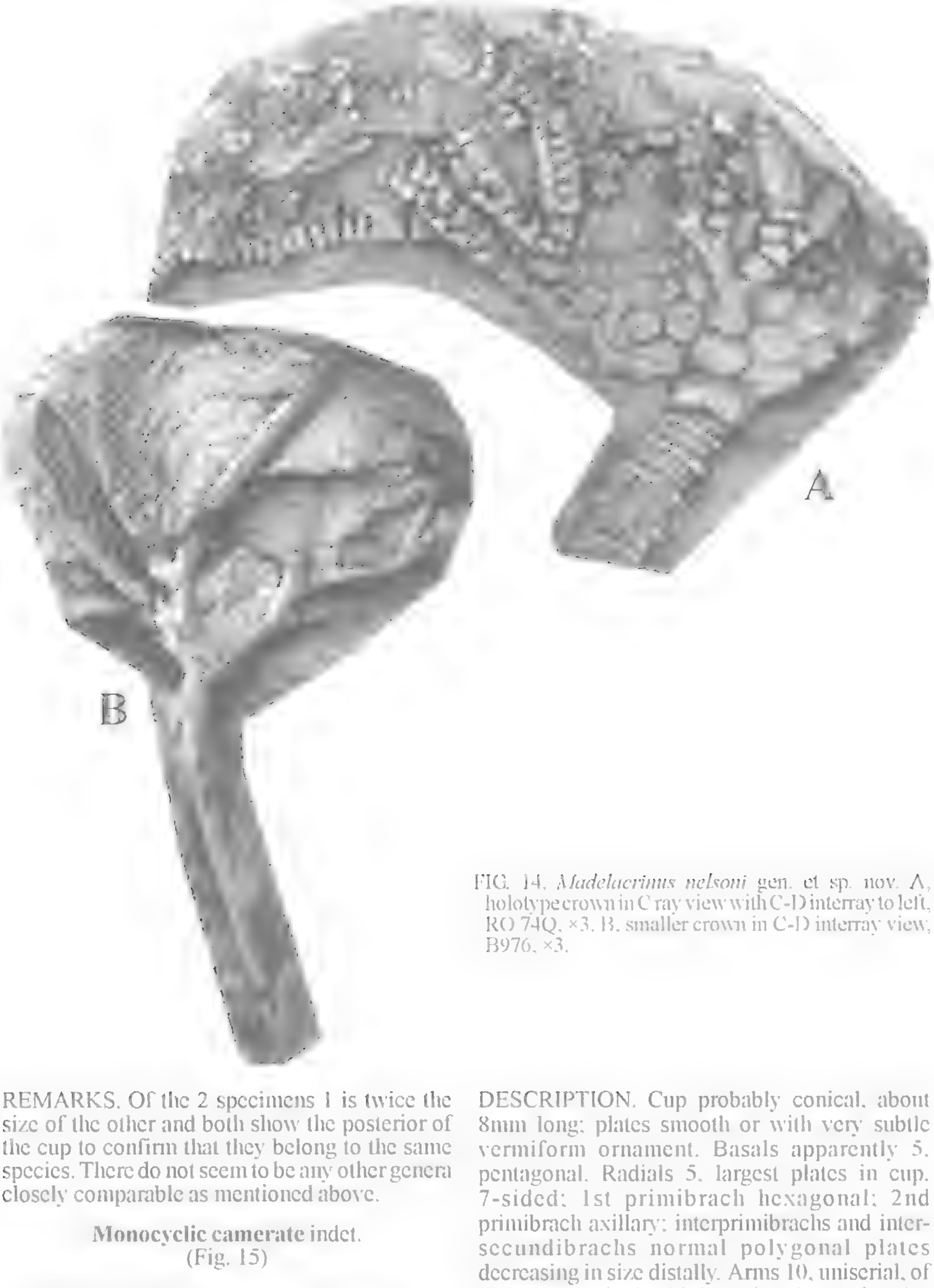



FIG. 14. *Madelacrinus nelsoni* gen. et sp. nov. A, holotype crown in C ray view with C-D interray to left, RO 74Q, ×3. B, smaller crown in C-D interray view, B976, ×3.

REMARKS. Of the 2 specimens 1 is twice the size of the other and both show the posterior of the cup to confirm that they belong to the same species. There do not seem to be any other genera closely comparable as mentioned above.

**Monocyclic camerate** indet.
(Fig. 15)

MATERIAL. PRV HR-5 from the Hex River area.

DESCRIPTION. Cup probably conical, about 8mm long; plates smooth or with very subtle vermiform ornament. Basals apparently 5, pentagonal. Radials 5, largest plates in cup, 7-sided; 1st primibrach hexagonal; 2nd primibrach axillary; interprimibrachs and intersecundibrachs normal polygonal plates decreasing in size distally. Arms 10, uniserial, of cuneate brachials, highly pinnulate; pinnules

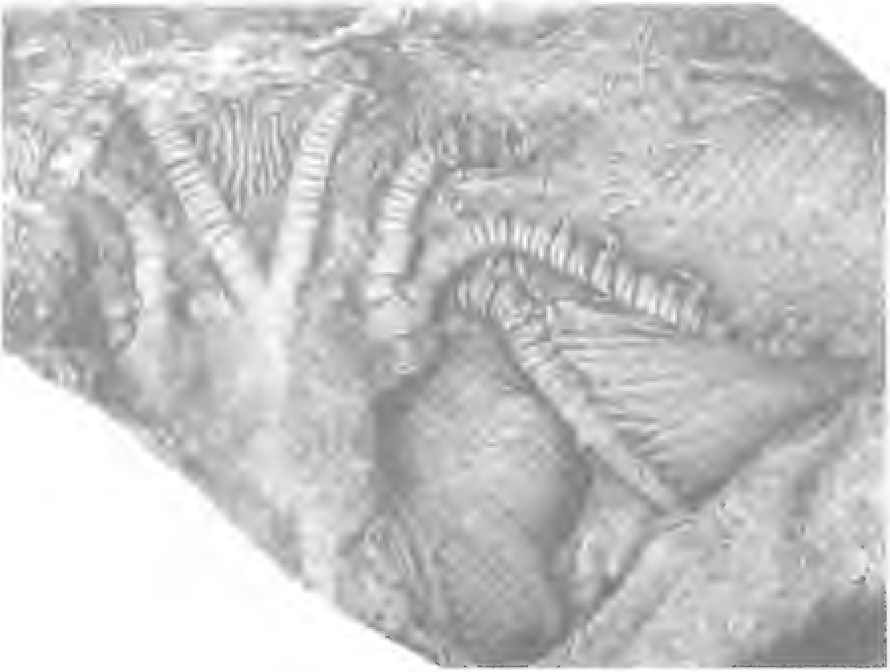


FIG. 15. Monocyclic camerate indet. Crown showing long pinnules and triangular brachials, PRV HR-5, ×4.

alternating from side to side on long side of brachials.

REMARKS. Without details of the posterior it is not possible to classify this specimen, but the large radials suggest an advanced compsocrinine group such as the Carpocrinidae and comparison, with for example *Acacocrinus* Wachsmuth & Springer,1897 (see Ubaghs, 1978, fig. 272.2), show complete correspondence in all features available from the South African specimen. Ausich (1987) transferred *Acacocrinus* to the Periechocrinidae but considered it a likely ancestor of the Carpocrinidae. Identification of the South African species must await further material.

Superfamily HEXACRINITOIDEA Wachsmuth & Springer,1885
Family HEXACRINITIDAE Wachsmuth & Springer,1885
**Arthroacantha** Williams, 1883

TYPE SPECIES. *Arthroacantha ithacensis* Williams, 1883 from the Upper Devonian of New York; by original designation.

**Arthroacantha**? sp.
(Fig. 16)

MATERIAL. One set of 5 incomplete arms RO128 (part and counterpart) from Gamkapoort, Prince Albert (33°18'S, 21°38'E) in the Gydo Formation.

DESCRIPTION. Arms biserial, pinnulate, occasionally with pair of adjacent 1/2 brachials extending into strong lateral spines, occasionally with other pairs of brachials in between spinose ones bearing circular facets; pinnules long, slender, with wide groove on inner surface; adoral groove on arm moderately deep, U-shaped in section; each brachial with concave pinnular facet.

REMARKS. Identity of thes arms is very doubtful but among known spinose genera *Arthroacantha* appears to have the most similar organisation (Kesling & Chilman, 1975, pl. 135) with periodic pairs of strong spines of the same dimension and arrangement as in our specimen. However, our arms do not appear to branch at the spinose brachials which is usual in *Arthroacantha*. Nevertheless, Stewart (1940:56) noted that in a specimen from the Silica Shale at Silica, Ohio large strong tubercles are irregularly developed between the bifurcations. Goldring (1923: 290) noted a subspinose tubercle on each

1/2 brachial above the axillary secundibrach in *A. carpenteri* Hinde, 1885. There is considerable variation in the arms of *Arthroacantha* so our specimen fits within the range. However, the assignment must be extremely tentative without knowledge of the cup; an alternative is that these arms may belong to a new crinoid genus.

Subclass CLADIDA Moore & Laudon, 1943
Order DENDROCRINIDA Bather, 1899

McIntosh (1983, 1986) discussed phylogeny and classification of dicyclic cladid inadunates and concluded that the 2 suborders of Moore & Laudon (1943) and 3 suborders of Moore et al. (1978) need major review. Until that review is complete we retain all the cladids in this paper in one broad group.

Family DENDROCRINIDAE
Wachsmuth & Springer, 1886

**Eckidocrinus** gen. nov.

TYPE SPECIES. *Eckidocrinus interbrachiatus* sp. nov.

ETYMOLOGY. An anagram from the surname of Mr Roy Dick, who contributed much material to this study.

DIAGNOSIS. Basals hexagonal, with broad low radial ridge ornament. Radial facet >1/2 radial width, gently declivate, concave. Interprimibrach depressed, filling interradial space between primibrachs. Arms with 2 main rami per ray, with bilateral heterotomous branching; 3rd primibrach axillary; strong ramules alternating side to side along each arm from every 3rd or 4th brachial, each ramule dividing at least twice. Stem circular, large diameter, heteromorphic.

REMARKS. Among early Palaeozoic cladids bilaterally heterotomous arm branching is not widespread. Although not restricted to that family, the arm branching pattern resembles fairly closely that of the Ordovician dendrocrinid *Grenprisia* Moore, 1962 which also has brachials shaped the same as the new genus and small interprimibrachs. Family assignment is made on these tentative grounds and a specimen exhibiting the posterior of the cup will be necessary to be more definite. With available morphology it is established as a separate genus. If the similarities to *Grenprisia* are indicative of relationship it must be very distant as they are well separated in time but no other known cladid has the combination of features mentioned above.

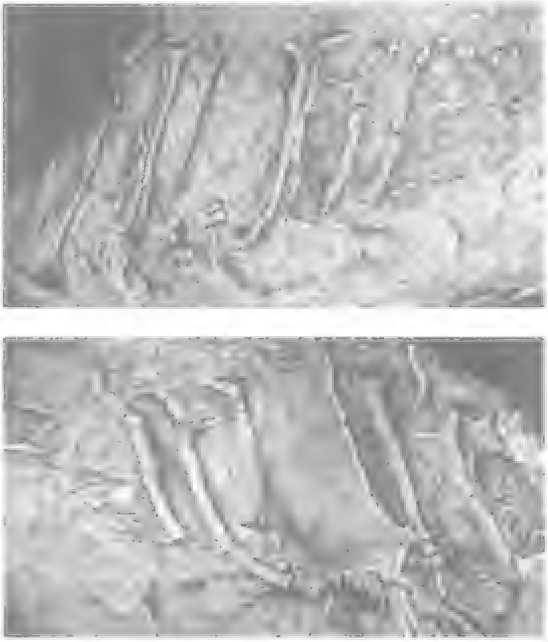


FIG. 16. *Arthroacantha*? sp., set of biserial arms with long pinnules and paired spines, RO 128a and b, ×1.5.

**Eckidocrinus interbrachiatus** sp. nov.
(Fig. 17)

MATERIAL. HOLOTYPE: B4534. PARATYPE: B4554 from the Voorstehoek Formation, at Matroosberg, Stinkfontein, Hex River Pass.

DIAGNOSIS. As for genus.

DESCRIPTION. Cup broadly conical (holotype 16mm max. diameter), short (holotype 9mm long); plates smooth, with broad low radial ridges and depressed corners in most parts of cup. Infrabasals 5, visible laterally, pentagonal, short, wider than long. Basals 5, largest plate in cup, hexagonal, with broad low ridges from infrabasals to radials and similar transverse ridge to adjoining basals, distal tip of basals depressed as are lateral parts, ridges less obvious at infrabasal to basal sutures. Radials 5, pentagonal, with scallop of radial facet in upper margin, with ridges running from basals towards facet and another similar ridge running laterally around cup near distal edge of radial circlet; radial facet >1/2 width of radials, a little less than semicircular, declivate, concave. Primibrachs 3, 2 subquadrate, wider than long; 3rd primibrach axillary, pentagonal. Interprimibrachs filling interradial notch to approximately base of 3rd

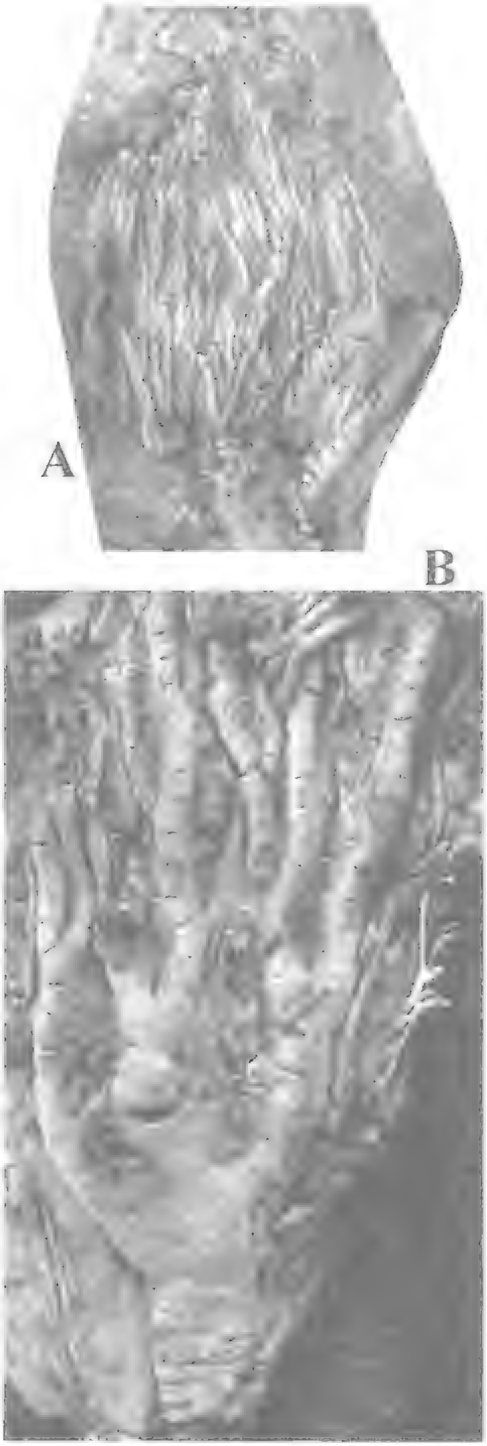



FIG. 17. *Eckidocrinus interbrachiatus* gen. et sp. nov. A, set of arms viewed from inside, B4554, ×1. B, holotype crown showing uniserial repeatedly branching arms, B4534, ×2.

primibrach plate, 3 larger plates resting on radials, becoming smaller distally. Arms bilaterally heterotomous, with 2 main arms per ray, with strong ramules (at least 6 per ramus) alternating from side to side along each arm at about every 3rd or 4th brachial, with ramuli dividing at least twice; full extent of arms not clear; ventral groove deep, broadly V-shaped in section, with large cover plate series, about 3 or 4 per brachial. Anal area of cup not available; anal sac longer than arms, straight, of small strongly ornamented plates, apparently perforated. Stem circular, heteromorphic, with noditaxis N3231323.

REMARKS. Part of the anal sac is preserved at the right of the arms in one specimen (Fig. 17A). The anal sac appears to have been long and composed of a few columns unornamented plates.

Family CYATHOCRINITIDAE Bassler, 1938
**Kopficrinus** Goldring, 1954

TYPE SPECIES. *Kopficrinus pustuliferus* Goldring, 1954 from the Lower Devonian of New York; by original designation.

REMARKS. Goldring's genus, for which the anal structure has been unknown except for the anal X supporting 3 small anals, was assigned to the Gasterocomidae by Moore et al. (1978) which family lacks an anal tube and has the anal opening through the side of the cup below the posterior radials. Thus the anal opening somewhere above the cup in the type species does not fit the family concept. The second species of the genus, described herein, with a long anal tube also argues against assignment to Gasterocomidae. We assign the genus to the Cyathocrinitidae based on the symmetrical anal plating, anal tube, the small pentagonal infrabasal circlet and the enlarged posterior basal.

**Kopficrinus halbichi** sp. nov.
(Fig. 18)

*Ophiurites* sp. Rossouw, 1933: 75, fig.2.

ETYMOLOGY. For Prof. I.W. Halbich, Stellenbosch University, who kindly made this material available.

MATERIAL. HOLOTYPE: SUK466. PARATYPE: SUK464 (2 specimens on one piece of rock (1 drawn by Rossouw, 1933), from the first shale band on Vredenhof, Prince Albert (locality quoted by Rossouw (1933) in the Gydo Formation.

DIAGNOSIS. Infrabasal circlet apparently fused; arms atomous (or with at least 14

primibrachs); anal sac of 4 columns of hexagonal sutured plates.

DESCRIPTION. Cup low, bowl-shaped, smooth. Infrabasal circlet pentagonal, apparently fused into a single plate, most of circlet visible in side view. Basals 5, pentagonal except for hexagonal posterior basal. Radials 5, with narrow angustary and declivate horseshoe-shaped facets, without axial canal separate from ventral groove. Anal X in radial circlet, slightly proximal to adjacent radials, resting symmetrically on posterior basal, with horizontal distal margin supporting 3 small anal plates at base of tall anal tube. Anal tube of 4 columns of close-packed hexagonal plates (distal end and anal opening not clear). Arms atomous (longest section available 14 brachials long). Stem circular in section, with vaguely pentalobate lumen.

REMARKS. Rossouw (1933, fig.2) gave a line drawing only of the specimen he identified as an ophiuroid and which is here designated a paratype of this new crinoid species. The line drawing was inaccurate in several details which are corrected here with a photograph (Fig. 18C,D); for example the specimen shows 3 of the 4 columns of plates in the anal tube whereas Rossouw's figure shows only 2. The latex cast from the counterpart of Rossouw's specimen gives the oral aspect, with the mouth area unclear; oral plates are not clear but may be assumed to have been present from the edges of the radials.

This species is assigned to *Kopficrinus* based on the matching posterior plating of the cup, the radial facets, the large round brachials and in particular the apparently atomous arms. Distal tip of any arm is not available in either the type or the new species but in both, arm sections are known with 13 or 14 brachials. Thus it is uncertain if the arms are atomous or not but it seems unlikely, from comparison with other crinoids, that these arms would divide for the first time so far from the cup; we consider the arms were most likely atomous.

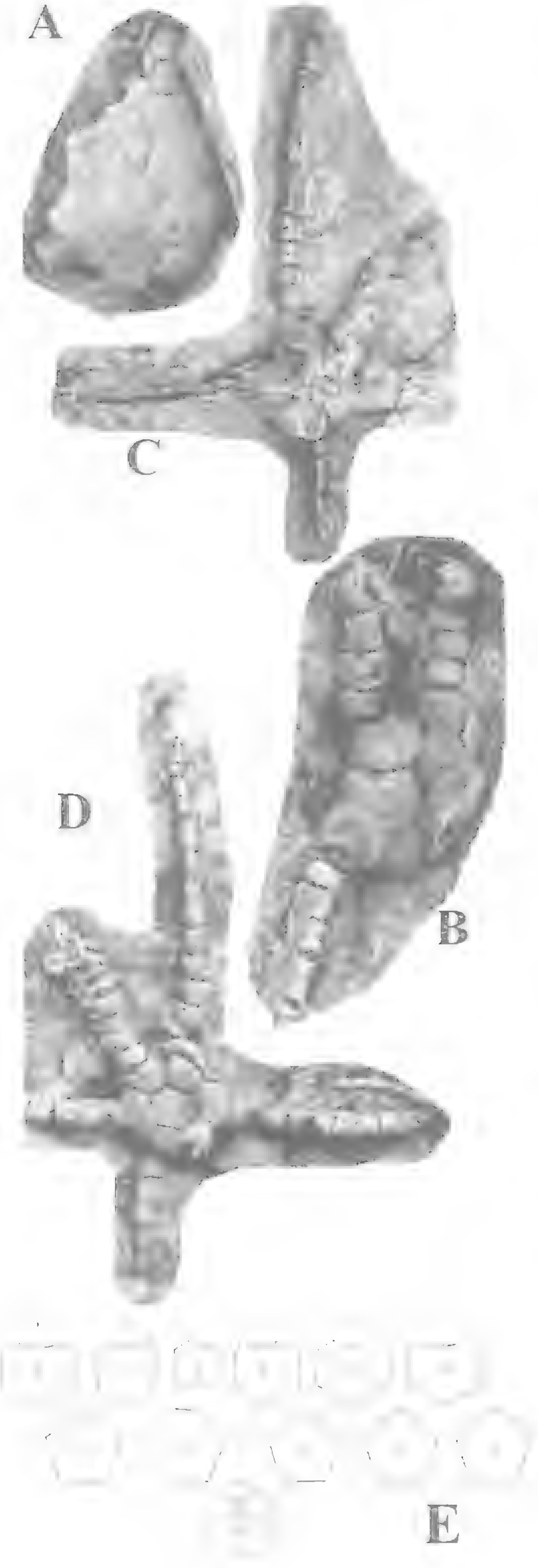


FIG. 18. *Kopficrinus halbichi* sp. nov. A, cup showing infrabasal circlet and anal tube (12 o'clock), SUG464. ×4. B, cup SUG464-1, ×4. C-D, oral and basal views of holotype cup SUG466a and b, ×3.5. E, sketch of plate arrangement with infrabasals shown as circlet with size of stem facet and section of central canal indicated. IB = infrabasal; B = basal; R = radial; X = anal X; A-E above radials indicate rays.

Family EUSPIROCRINIDAE Bather, 1890
**Monaldicrinus** gen. nov.

TYPE SPECIES. *Monaldicrinus johni* sp. nov.

ETYMOLOGY. An anagram for John Almond, Geological Survey of South Africa, Capetown, who greatly assisted us during this project.

DIAGNOSIS. Cup low, strongly flared laterally. Infrabasals 5. Basals 5. Posterior basal heptagonal, supporting 2 almost equally sized anal plates distally. C radial virtually symmetrical distal to BC basal. Anal sac large and long, with opening at tip, with main column of plates both externally and adaxially. Arms 10, uniserial, stout, dividing isotomously once, ramulate; ramules alternating from side to side on every 5th brachial, dividing isotomously on 6th tertibrach. Stem circular in section, small diameter for the family, with moderately large lumen vaguely pentalobate in section.

REMARKS. This genus is assigned to the Euspirocrinidae on the arrangement of anal plates in the cup which arrangement compares closely with *Parisocrinus* Wachsmuth & Springer,1880 and *Ampheristocrinus* Hall,1879, on the nonpinnulate arms, on the 5 infrabasals and basals, on the ambulacral groove cover plates and on the circular stem. It is distinctive in its arms branching only once isotomously, in being ramulate and their arrangement, in the nature of the large anal sac, in the low flared shape of the cup which does approach *Vasocrinus* Lyon,1857 and in the relative diameter of arm to stem. The anal plate arrangement is also found in *Poteriocrinites* (see Moore *et al.*,1978, fig.394.7) but that genus of the Poteriocrinina has pinnulate arms which is used by Moore *et al.* (1978) as a subordinal discriminator. The arm structure of *Monaldicrinus* occurs in the Barycrinidae but that family has a distinctly different anal plate arrangement. However, in discussing the Barycrinidae, Moore & Laudon (1943:40) considered the single isotomous branching followed by development of alternating ramules (their branchlets) to be a primitive stage of development leading to pinnulation. They also considered the transverse ridge on the articular facet, seen in *Monaldicrinus*, an advanced feature. It is tempting to suggest that perhaps *Monaldicrinus* from the Malvinokaffric Province was an advanced cyathocrininid ancestral to the Poteriocrinina.

**Monaldicrinus johni** sp. nov.
(Figs 19-21)

MATERIAL. HOLOTYPE: SAMK977, an external mould from 100m N of the house at Wolfaardt's Farm, Riet Valley, near Ceres. PARATYPES: B4579 from Hex River Pass, 1.3 miles from Great Swaarmoed Farm; SAM3947 from Laken Vlei, Ceres (1st Shale); RO202 and 810 from Gamkapoort, Prince Albert, 33°18'S, 21°38'E (C2S1).

DIAGNOSIS. As for genus.

DESCRIPTION. Cup smooth, small relative to size of crown, 15mm long, conical. Arms apparently elevated only 10-20° above horizontal. Infrabasals 5, pentagonal, uniform in size, almost completely visible and as long as wide in side view. Basals 5, hexagonal except for heptagonal BC and CD basals, base against infrabasals with obtuse angle (>150°) at central junction with suture between infrabasals. Radials 5, large, wider than long, heptagonal; radial facet only slightly declined outwards, peneplenary. Facet on 1st primibrach with strong transverse ridge broken by central gap, with large circular canal just beneath broadly V-shaped ambulacral canal. Circular canal migrating through the gap in transverse ridge by 5th primibrach to be close to outer edge of facet and well removed from sharply V-shaped ambulacral groove. Ambulacral groove covered by thick cover plates; cover plates more numerous than brachials (c. 8 to 5) but exact correspondence unclear. CD basal supporting hexagonal anal X and pentagonal radianal; radianal resting symmetrically on BC and CD basals, supporting the right tube plate (3rd anal plate in cup) adjacent to the C ray. Anal sac large, with terminal aperture, with numerous (>10) vertical columns of polygonal plates; some columns with plates having scalloped lateral margins (scallops never on proximal or distal margins) with perforations through wall at each scallop; perforations most prominent near base disappearing before tip; main column of larger plates on outer side distal to anal X and on inner side rising from oral area; main column on inner side with short stubby spine usually on every 2nd plate but irregular and sometimes on consecutive plates; such spines less frequent and more irregular on some other columns on inner side but not on outer side of sac. Arms 10, each ray with 1 isotomous branching at axillary primibrach 8 (B4579)-12(RO810). Above this 1 specimen (RO202) with ramules developed alternately on each 5th secundibrach; 1st ramule on outside of ray; ramule branching isotomously at least twice

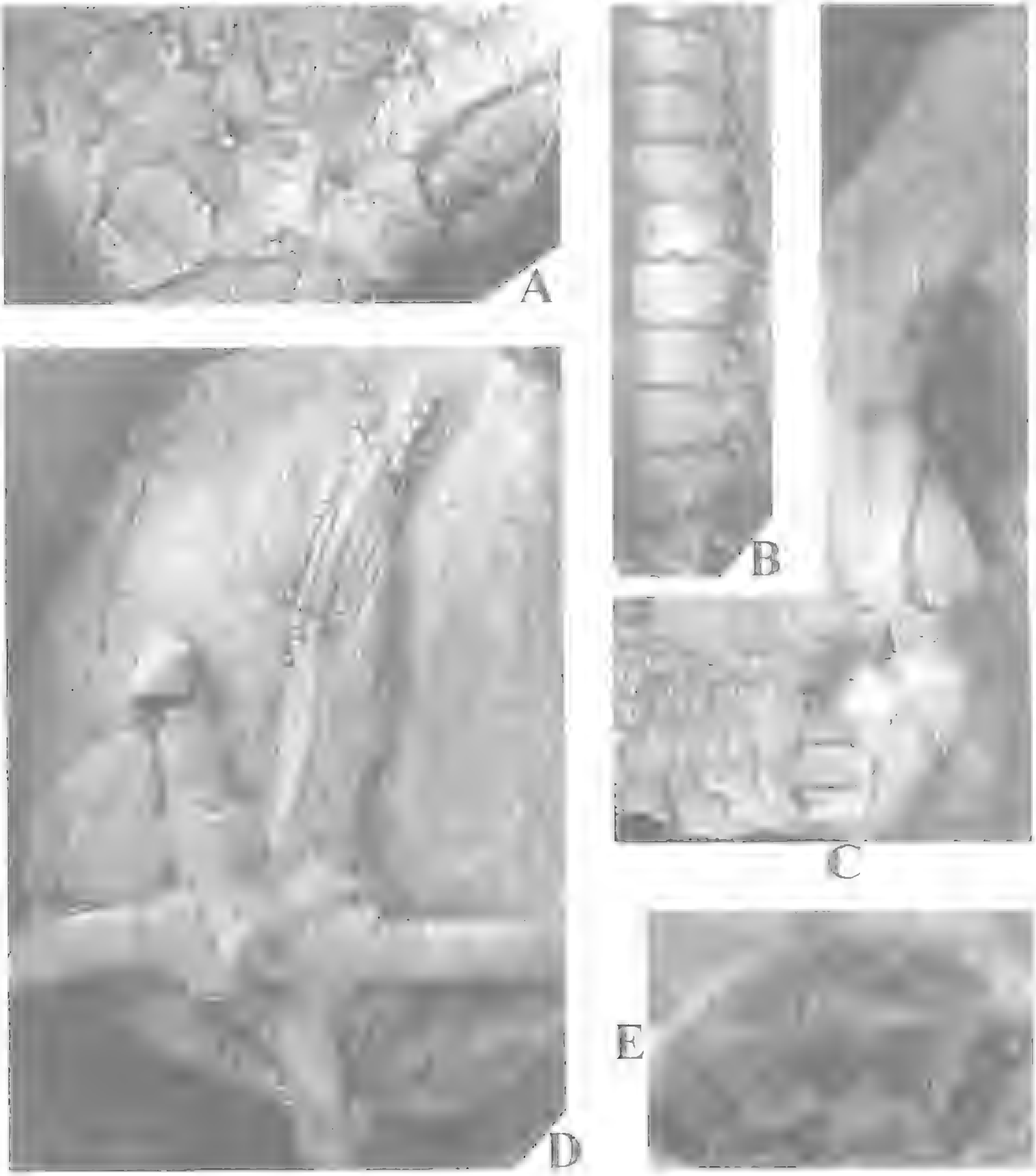



FIG. 19. *Monaldicrinus johni* gen. et sp. nov. A,C,E, RO 810. A, cup ×2. C, cup showing stout uniserial arm, ×1.2. E, distal face of first primibrach ×6. B, part of an arm showing ambulacral cover plates B4549, ×6. D, holotype SAM K977, ×2.

each time at 5th brachial, circular in section, shorter than 4 secundibrachs, standing up vertically off the arm. Stem circular in section, small diameter for the family and relative to cup, with moderately large lumen vaguely pentalobate in section.

REMARKS. The 4 specimens of the cup have the arms splayed out horizontally or almost so, mostly in the bedding plane. Also in each is a

degree of dislocation and dislodgement along sutures and fracture across plates within the cup. These taphonomic features make it difficult to interpret original cup shape and arm attitude. In so far as the plates are in contact around the cup at the radial circlet we could interpret minor flattening of the cup. However, in Fig. 19D where the anal sac is assumed to have been vertical in life but is now horizontal, the dislocation of plates near its base is minimal and certainly does not suggest such a change in attitude after death. We therefore, have no reason to believe the horizontal arm position reflects the original attitude. While it is more likely, by comparison with other cladids, that the arms were erect, the much smaller stem diameter, relative to crown size in *Monaldicrinus* which is a fairly large crown among crinoids in general may suggest either 1, it lived in quiet water and so did not need strong attachment in currents (unlikely given the enclosing clastic sediments but nevertheless the animal is found in the finer shale layers and may have migrated with the environment) or 2, that the arms were less erect and thus less of a baffle to currents. What ever the answer, we consider that the arms were probably not completely erect but that the ramules coming off them were probably vertical. In the 3 specimens with 4 rays preserved the A ray is missing and the plating near its base is unclear. In Fig. 19D there is the suggestion that it may lie on the basals but with only point contact to the other radials rather than a sutured junction of some length. We cannot be certain of this point due to preservation but if so this would provide a strong accentuation of the A ray - CD interray line of symmetry.

FIG. 20. *Monaldicrinus johni* gen. et sp. nov. sketch of plate arrangement (infrabasals shown as circlet with size of stem facet and section of central canal indicated) and arm branching (on right). IBB = infrabasal circlet; B = basal; R = radial; RA = radianal; X = anal X; rt = right tube plate; A-E above radials indicate rays.

The large specimen of the oral side of the arms and anal sac (Fig. 21C) is assigned to this species on the nature of the anal sac, size and nature of the arms and their branching pattern. Although very difficult to see on the latexes, ramules are identified on the mould of Fig. 21B (because of the penetration of limonite) at every 5th secundibrach. The prominent tubercles on that specimen which are lacking on other specimens are interpreted as only occurring on the oral side of the anal sac and thus not evident on the other specimens of the outer side. Without moulds of the 2 sides from the 1 individual this cannot be confirmed. Until it is determined objectively we remain confident of our identification.

## Family THALAMOCRINIDAE Miller & Gurley, 1895

Following McIntosh & Brett (1988) this family name replaces Bactrocrinitidae Jaekel, 1918 as used by McIntosh (1979; 1983). *Sacrinus* is assigned to this family based on its affinity to *Follicrinus* which was assigned to the Bactrocrinitidae by McIntosh (1979, 1983) and although excluded by McIntosh & Brett (1988) is retained in the family herein. Family level subdivision of the cladids remains in flux so we adopt a broad family concept here. We acknowledge that quadrangular vs. pentagonal radianal plate could indicate entirely separate lineages but this has not been demonstrated and is not applied herein.

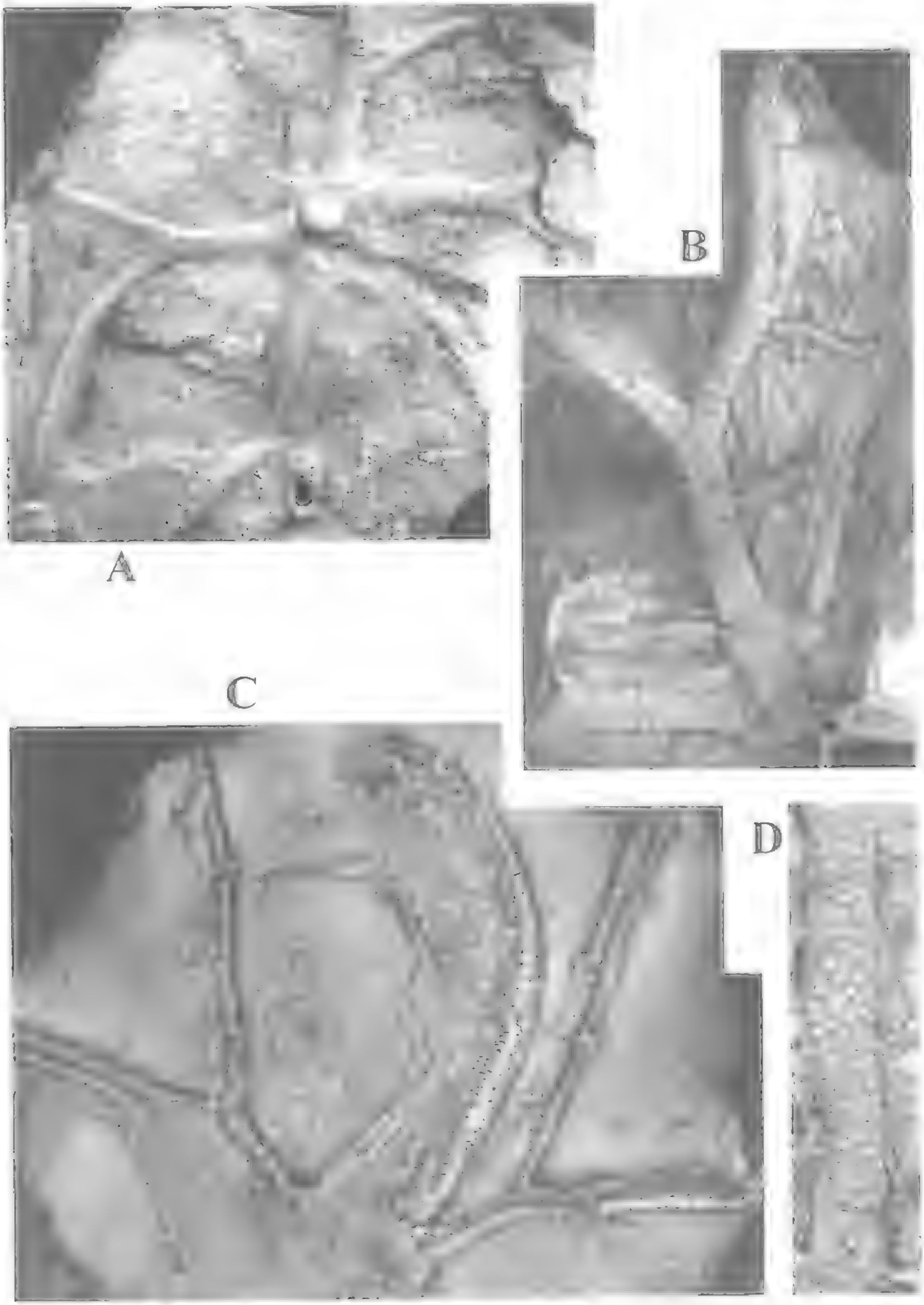
### **Sacrinus** gen. nov.

TYPE SPECIES. *Sacrinus gamkaensis* sp. nov.

ETYMOLOGY. Sa- for South Africa.

DIAGNOSIS. Cup conical; infrabasals approximately same length (or only slightly shorter) as basals; radials wider than long, with angustary radial facets projecting laterally. Anal plates in cup 3, with broad low radial ridge

FIG. 21. A-C, *Monaldicrinus johni* gen. et sp. nov. A, crown splayed on bedding plane in proximal view, SAM3947, ×1. B, crown showing anal tube on right B4579, ×2. C, set of arms showing cover plates and widely spaced ramules and large anal tube RO 202, ×1. D, stem indet., section of distinctive indeterminate stem in lateral view RO 295a, ×4.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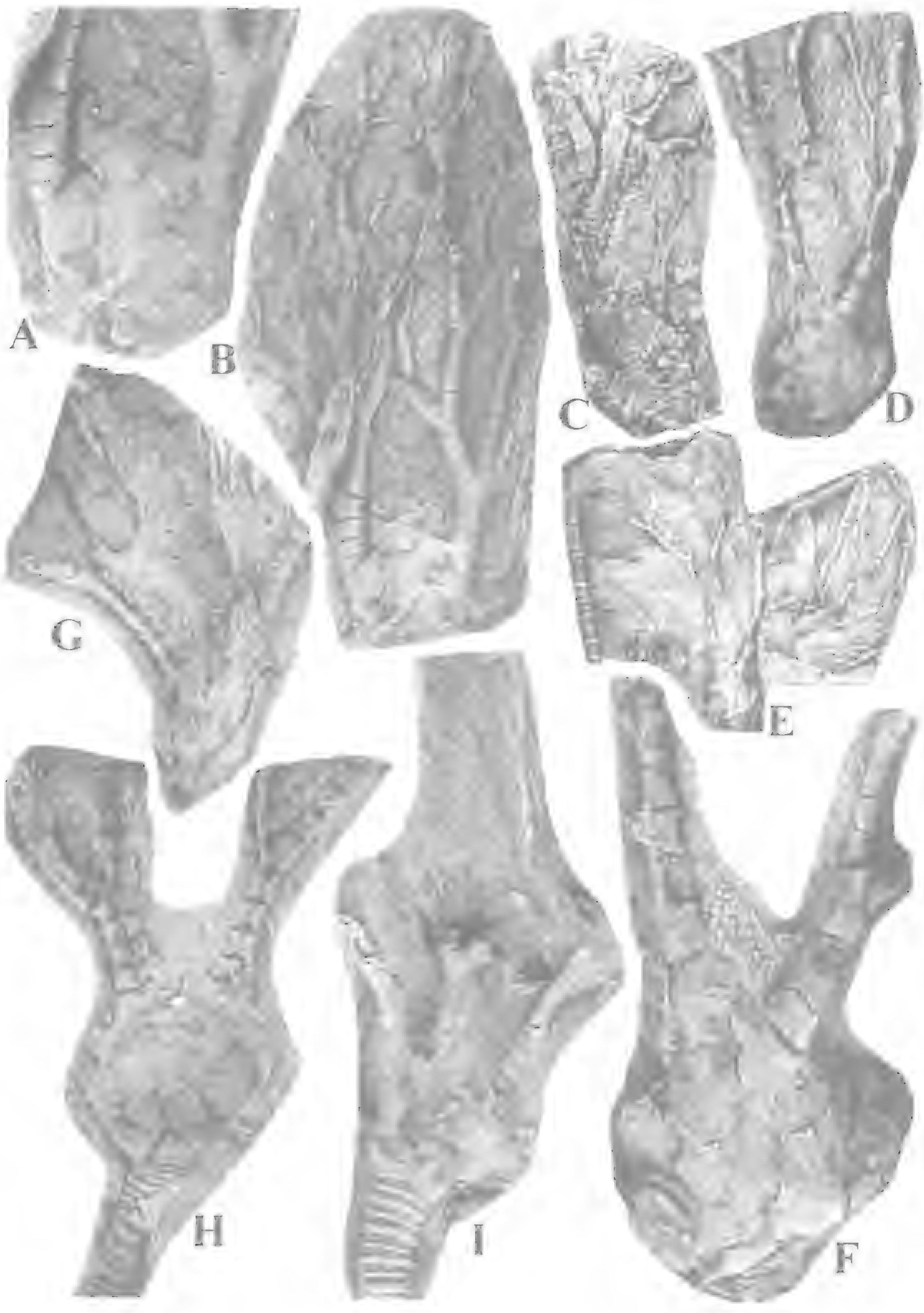
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FIG. 23. *Sacrinus gamkaensis* gen. et sp. nov., sketch of plate arrangement and arm branching (on right) with distal branching shown on only one branch but symmetrical on each other branch. IB = infrabasal; B = basal; R = radial; RA = radianal; X = anal X; rt = right tube plate; A-E above radials indicate rays.

ornament; radianal pentagonal, proximal and left of C radial, directly supporting right tube plate; anal X not much larger than radianal; anal tube large, inflated, irregularly shaped, of many very small polygonal plates irregularly arranged. Arms robust, branching isotomously 3 or 4 times. Stem pentagonal to subrounded in section, heteromorphic.

REMARKS. The major distinguishing feature of this new genus and of *Follicrinus* Schmidt, 1934 (type *Taxocrinus? grebei* Follmann, 1887) from the Lower Devonian of Germany is the irregularly shaped, inflated anal sac of small irregularly arranged stellate plates. McIntosh (1983) queried whether this feature alone should carry generic status, particularly in the absence of knowledge of the anal sac in *Bactrocrinites fusiformis* Roemer, 1844, the type of *Bactrocrinites*. In *Follicrinus* the radianal is quadrate, there are only 2 anal plates in the cup, the radial facets may be interpreted as plenary (as by Moore et al. (1978) who clearly thought so by placing it in the Mastigocrinidae) and the stem is circular in section and composed of long columnals. In *Sacrinus* the radianal is pentagonal, there are 3 anal plates in the cup, radial facets are clearly peneplenary and protruding and the stem is heteromorphic and pentagonal in section. Despite these differences cup shape including shape and proportions of most individual plates, robustness and branching of the arms, size and plate ornament and arrangement of the anal sac and tuberculate ambulacral cover plates indicate a fairly close relationship between the 2 genera. We note some comparison with Ordovician *Grenprisia* Moore, 1962 in the very large cylindrical to inflated anal sac of small stellate or smooth plates, the 5- or 6-sided radianal, short wide radials and pentagonal stem. However, these comparisons could very well reflect parallel evolution and without intermediate forms no suggestion of affinity is made. The distinctive anal structure makes comparison with other cladids rather unnecessary.

**Sacrinus gamkaensis** sp. nov.
(Figs 22-25)

ETYMOLOGY. From Gamkapoort.

MATERIAL. HOLOTYPE: ROC25. PARATYPES: RO127, 255, 731, L7, C25, B4522, B4523, B4526, B4527 and B4530 all from Gamkapoort, all from the Gydo Formation. OTHER MATERIAL: B4574 from the Hex River Pass area on Montagu Road, 14km from the N9 turnoff; RO283 from Swaarmoed Pass, Ceres, 33°21'30"S, 19°30'30E; and ROT15 from Matroosberg, Worcester (Hex River Pass), 33°30'S, 19°49'E; all in the Voorstehoek Formation. B4669 from the quarry on E of road N from Prince Alfred's Hamlet, about 1km S of Gydo in the Gydo Formation.

DIAGNOSIS. Radials and basals with broad low ray ridges. Anal plates in cup 3; anal X only just larger than pentagonal radianal; anal plates and proximal anal sac plates with distinct ray ridges; anal sac long, cylindrical to moderately inflated, composed of many tiny stellate polygonal abutting plates. Arms isotomous, 1st branching on 4th, 5th, or 6th primibrach. Stem subpentagonal in section, heteromorphic.

DESCRIPTION. Cup conical, up to 5mm long, with broad low radial ridges and (in some specimens) ornament of fine lines on top of ridges. Infrabasals 5, pentagonal, slightly wider than long (max). Basals 5, hexagonal except for heptagonal BC basal, with radial ridges forming a broad cross. Radials wider than long; articulating facet angustary, about 0.5 of plate width, only slightly declined, almost circular, projecting

FIG. 22 *Sacrinus gamkaensis* gen. et sp. nov. A-B, crown in C-D interray view showing base of anal tube and arm branching RO 255, ×6 and ×4, respectively. C, anal tube and interior of some arms RO L7a, ×2. D-F, crown showing arm branching and ornament on cup RO C25, ×2, ×1 and ×3, respectively. G, crown showing anal tube, RO T21, ×3. H, interior view of crown RO 127, ×4. I, crown viewed from side opposite anal interray showing anal tube RO T18, ×3.

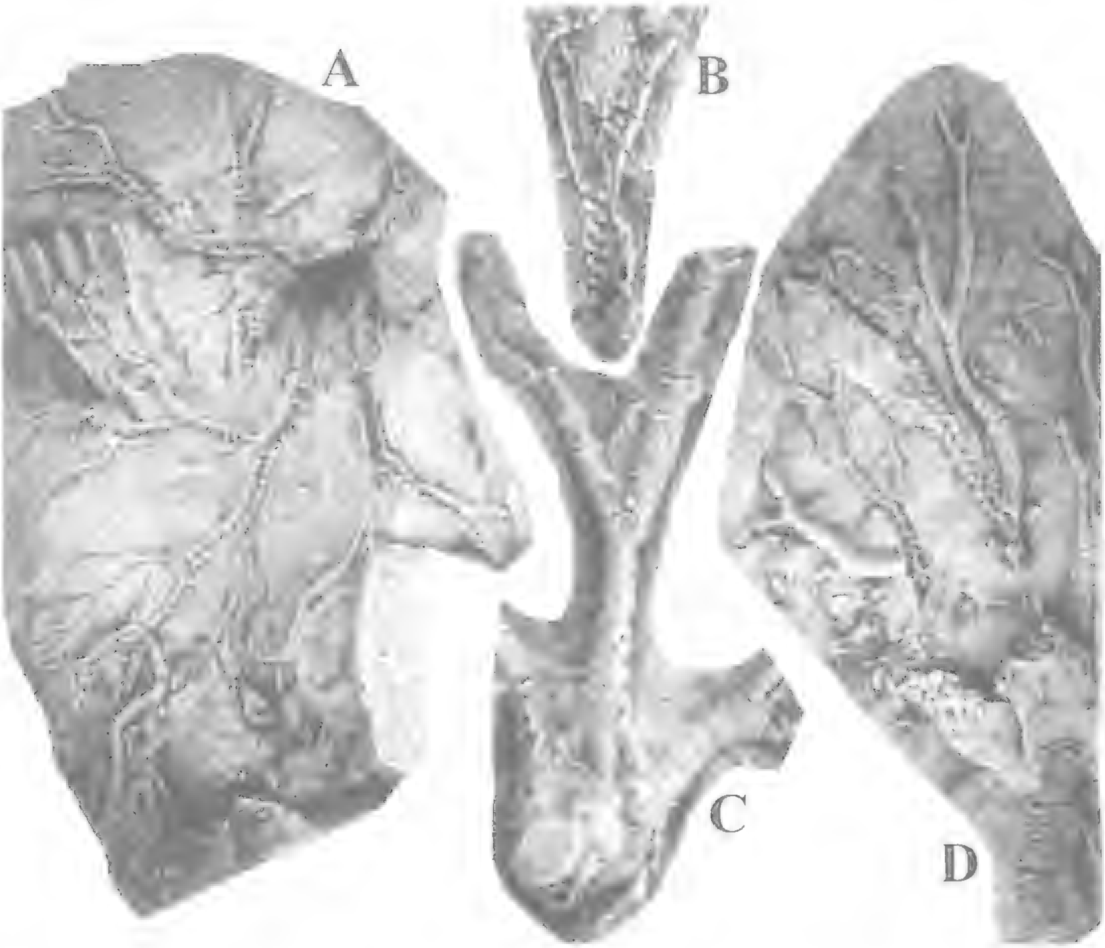



FIG. 24. *Sacrinus gamkaensis* gen. et sp. nov. A, crown in ambulacral view of arms and internal mould of cup RO 731, ×2. B, ambulacral view of arm showing small cover plates RO 255, ×5. C, partial crown showing ray ridges on radials RO T25, ×3. D, crown showing ornament on anal tube RO L7, ×3.

laterally; radial ridges radiating from arm base in 4 directions towards centre of 4 lower sides (i.e. 2 cross to adjoining basals and other 2 laterally onto adjoining radials or radianal in case of C radial). Anal plates in cup 3, with radiating ridges directed to the middle of each side, with all 3 way sutural junctions depressed; anal X hexagonal, directly distal to CD basal, contacting D radial and other 2 anal plates towards C ray; radianal pentagonal, proximal and left of C radial, contacting BC and CD basals; right tube plate directly distal to radianal. Anal sac subcylindrical, inflated irregularly, reaching distally to about 3rd arm division, of many tiny irregularly polygonal abutting plates, aperture not observed; each plate with radial ridge ornament continuing and becoming finer distally. Arms slender, branching isotomously 7 times, laterally compressed in cross section, with deep adoral groove, with column of tiny cover plates on either side of groove; primibrachs 4, 5 or 6 axillary; in 2nd and more distal brachial series 5th brachial usually axillary (variable between or within arms even in 1 specimen). Stem subcircular to subpentagonal in section, noditaxis N3231323, with latus projecting laterally on nodals.

REMARKS. *Sacrinus gamkaensis* is distinguished from *S. hexensis* by the radial ornament on its anal cup plates and anal sac, the latter being smooth. A few specimens of the type species also show a very fine multiple ridge ornament (Fig. 22D, F) on top of the broad radial ridge ornament that is the specific distinguisher. Some specimens

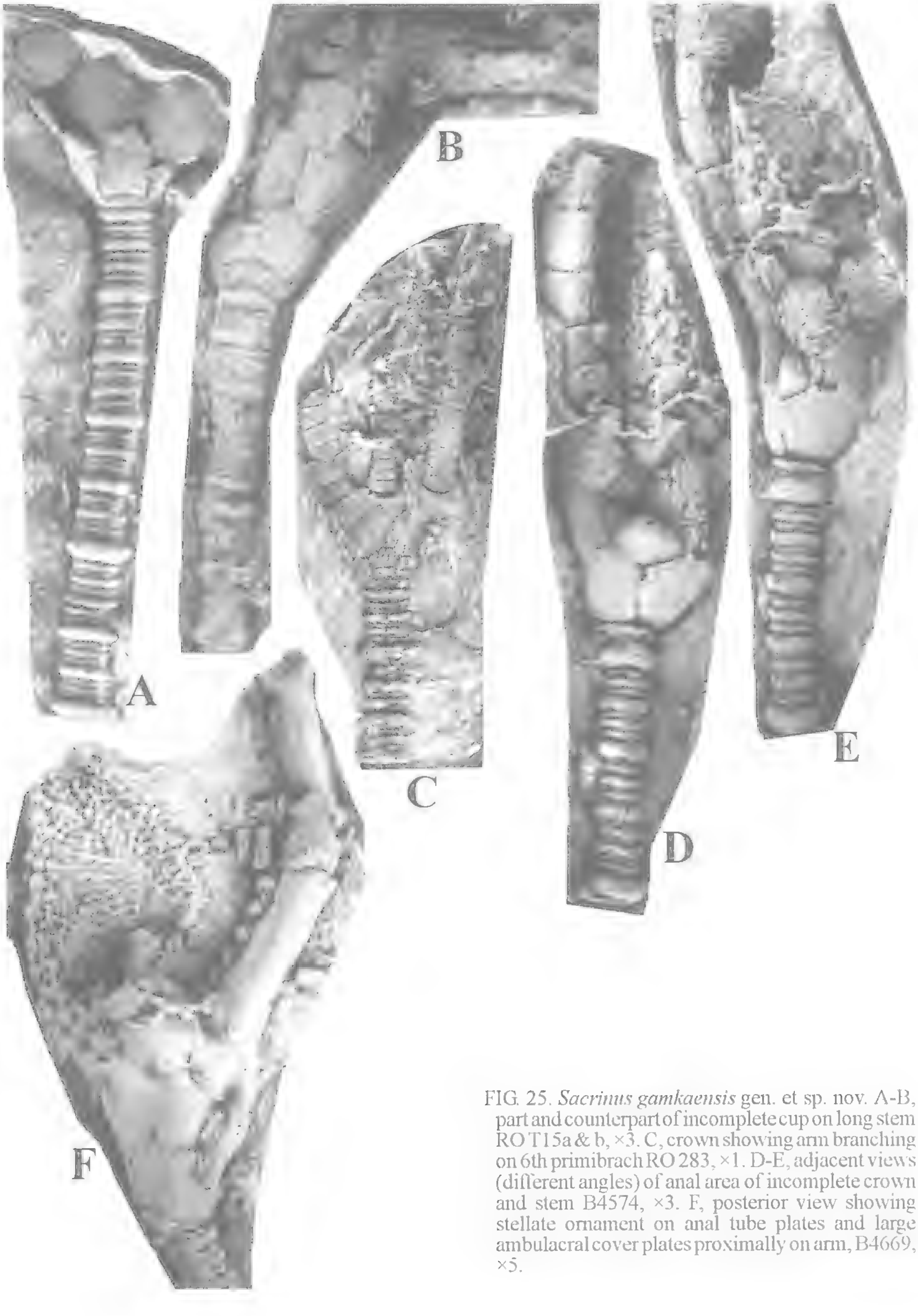
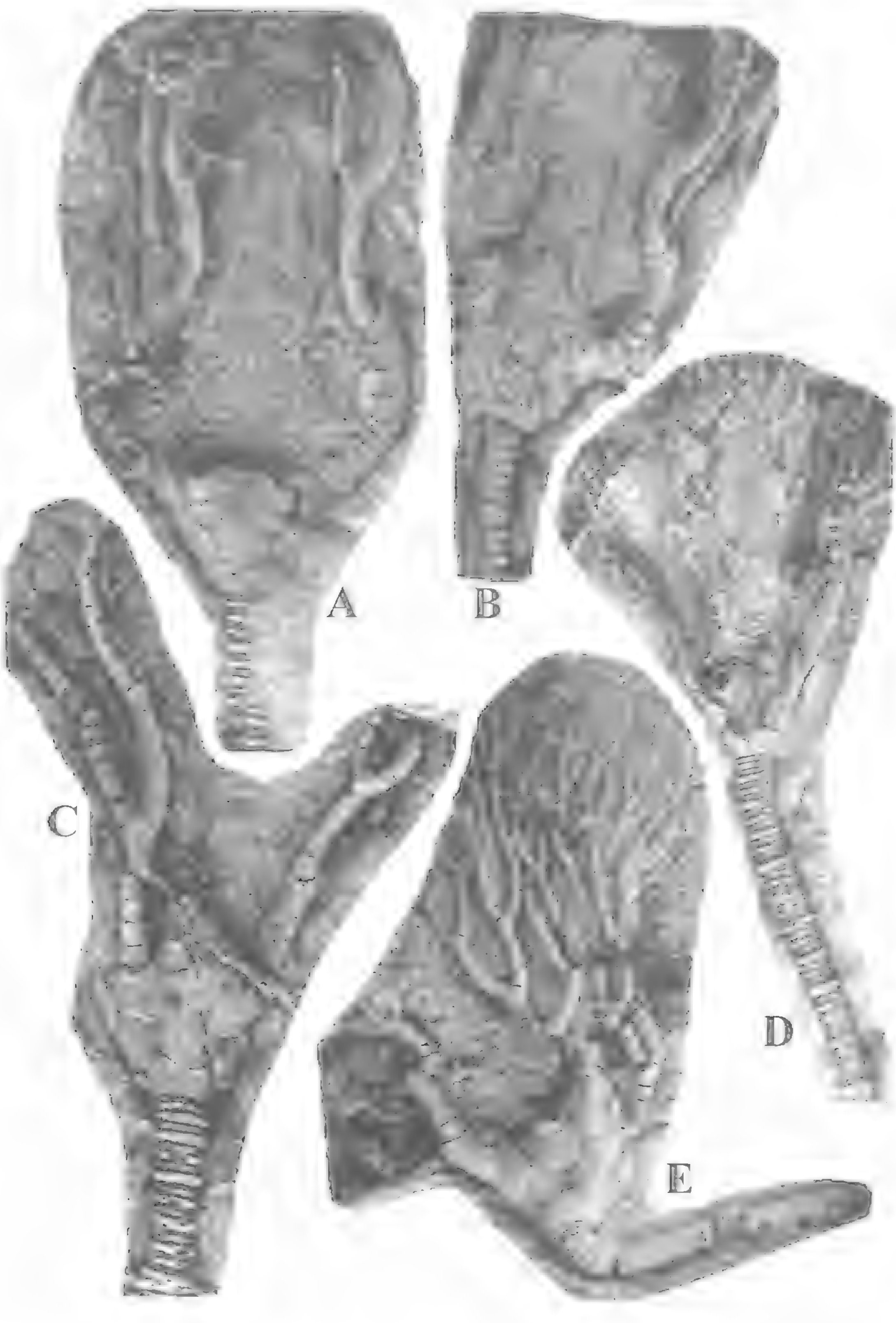


FIG. 25. *Sacrinus gamkaensis* gen. et sp. nov. A-B, part and counterpart of incomplete cup on long stem RO T15a & b, ×3. C, crown showing arm branching on 6th primibrach RO 283, ×1. D-E, adjacent views (different angles) of anal area of incomplete crown and stem B4574, ×3. F, posterior view showing stellate ornament on anal tube plates and large ambulacral cover plates proximally on arm, B4669, ×5.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E

(Figs 22A, 25C) suggest a pustulose surface on radial plates and in others (Fig. 24C) the radial ridge ornament is well developed on radials as well as anal cup plates. Variation noted here is considered intraspecific.

**Sacrinus hexensis** sp. nov.
(Fig. 26)

ETYMOLOGY. From the Hex River Pass

MATERIAL. HOLOTYPE: B4571a (lower specimen of 2 close together). PARATYPES: B4571b (other 2 specimens), B4572, PRV HR5 all from Hex River Pass on Montagu Road, 14km from N9 turnoff (C2S2).

DIAGNOSIS. Cup plates including anal plates and anal sac plates smooth; anal sac long, subcylindrical, of many small polygonal abutting plates; 1st arm branching variable at 3rd-6th primibrach.

DESCRIPTION. Cup short, conical, with smooth plates, up to 5mm long. Infrabasals 5, pentagonal, as long as wide (max). Basals 5, hexagonal except for heptagonal CD basal. Radials wider than long in lateral view, with 6 sides plus radial facet; radial facet angustary, about 0.5 of plate width, only slightly declined, almost circular. Anal plates in cup 3; anal X hexagonal, distal to CD basal, contacting D radial and other 2 anal plates towards C ray; radianal pentagonal, proximal and left of C radial, contacting BC and CD basals; right anal tube plate distal to radianal. Anal sac subcylindrical, reaching distally to about 3rd arm division, composed of many tiny smooth polygonal abutting plates, opening terminal, with circlet of elongate plates around aperture. Arms slender, branching isotomously 4 times, laterally compressed in cross section, with deep adoral groove, with columns of tiny cover plates on either side of groove; primibrachs 3, 5, 6 or 7 axillary; similar variation in subsequent brachial series, number of brachials between axillaries not consistent even within one specimen. Stem subpentagonal to subrounded, heteromorphic, noditaxis N3231323; nodals slightly longer and wider, with rounded latus.

REMARKS. This species is distinguished from *K. gamkaensis* above.

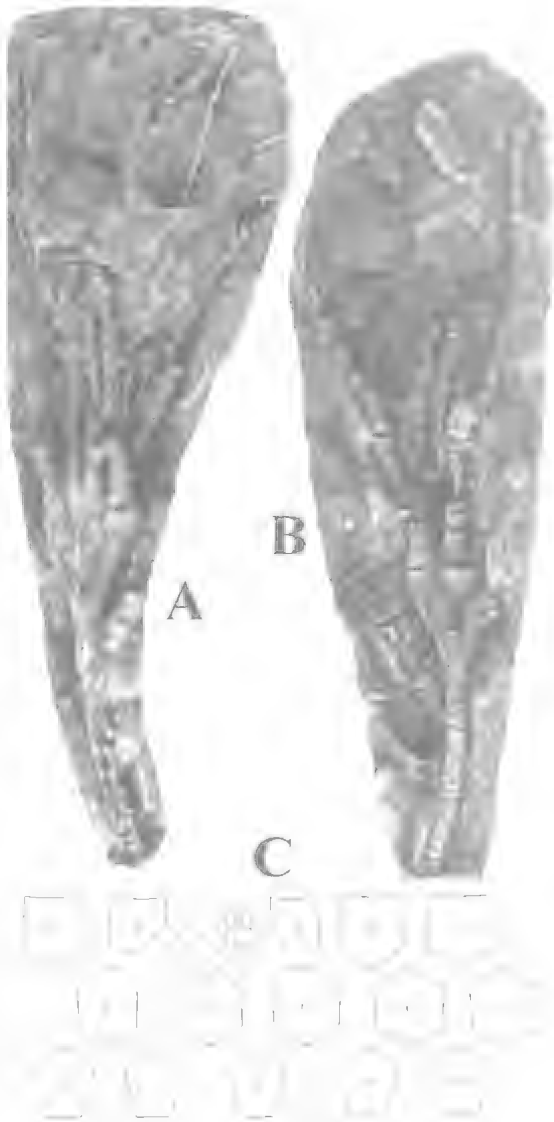



FIG. 27. *Cradeocrinus plenarius* sp. nov. A-B, holotype crown B207A, ×5. C, sketch of plate arrangement. IB = infrabasal; B = basal; R = radial; RA = radianal; X = anal X; rt = right tube plate.

**Cradeocrinus** Goldring, 1923

TYPE SPECIES. *Cradeocrinus elongatus* Goldring, 1923 from the Upper Devonian West Falls Group of western New York; by original designation.

FIG. 26. *Sacrinus hexensis* gen. et sp. nov. A, crown showing anal tube from side of cup opposite C-D interray B4571c, ×5. B- C, holotype crown in A ray and C-D interray views B4571a & b, ×4, respectively. D, crown in A-E interray view B4571D, ×3. E, crown with D radial central and anal cup plates to right HR-5, ×5.

**Cradeocrinus plenarius** sp. nov.
(Fig. 27)

ETYMOLOGY. For the plenary radial facets.

MATERIAL. HOLOTYPE: B0207 from the Waboomberg Formation at Boplaas Farm, N of Ceres.

DIAGNOSIS. Cup long, cylindrical, very small; plates smooth. Radial facets plenary. Three anal plates in cup; radianal pentagonal, contacting 1st right tube plate; anal sac long slender, of 8-10 columns of polygonal plates, perforated in sutures. Arms slender, of long brachials with shallow ventral groove, branching isotomously at 4th primibrach.

DESCRIPTION. Cup small, 2.2mm long, 1.2mm max diameter, high conical; plates smooth. Infrabasals 5, equal, long, pentagonal in lateral view. Basals 5, hexagonal, longest plates in cup. Radials 5, pentagonal, with plenary radial facets. CD interray wide, with 3 anal plates in cup, and proximal 1/2 of 2 others just in cup, anal X and radianal each supporting column of plates rising into anal sac; radianal pentagonal, proximal and left of C radial, contacting right tube plate; anal sac at least 10mm long, of 8-10 columns of regular hexagonal plates, with depressions leading to perforations in the sutures. Arms very slender, tapering strongly over 1st 2 primibrachs, long (longest available incomplete at 19mm), with 4th primibrach axillary, branching at least twice distally but type of subsequent branching uncertain (probably heterotomous with ramules from shapes of axillaries available), non-pinnulate; primibrachs more than twice as long as wide, with shallow ventral groove. Stem circular in section, heteromorphic, with alternating long and short columnals of uniform diameter, tapering for proximal 10mm then uniform in diameter, full length unknown.

REMARKS. This species is distinguished in the genus by its plenary radial facets (other species have peneplenary facets), small size, smooth plates, and very slender arms. It has the cup shape of *C. elongatus* and the anal sac structure of *C. nanus* (Roemer,1863) (Schmidt,1934, fig.24) but in combination its features are separate.

**Thalamocrinus** Miller & Gurley, 1895

TYPE SPECIES. *Thalamocrinus ovatus* Miller & Gurley, 1895 from the Ludlovian Brownsport Formation in Tennessee; by origianal designation.

REMARKS. McIntosh & Brett (1988) reviewed the genus in detail providing a clear basis for comparison. The South African material is not as well preserved as most of the North American species and on only one South African specimen is the posterior interray available, and then not clearly. However, the radianal, although pentagonal is similarly placed and the anal X is in the radial circlet, the cup is barrel-shaped to only very slightly flaring, the plates are of similar thickness and the proximal part of the stem is very similar with nodals much larger than internodals and well rounded laterally. *T. arenaceus* is distinguished within the genus by its very short infrabasal circlet.

**Thalamocrinus arenaceus** sp. nov.
(Fig. 28)

ETYMOLOGY. For the sandstone matrix of all specimens.

MATERIAL. B4538 and B4556 (numerous cups and arm and stem fragments on each slab) from the Gamka Formation at Grootrivier Hoogte.

DIAGNOSIS. Infrabasals short in lateral view.

DESCRIPTION. Cup barrel-shaped to slightly flaring at radials, about as long as wide (6-8mm in available specimens); plates smooth, convex, thick. Infrabasals 5, very short and pentagonal in lateral view. Basals 5, hexagonal, as wide as long; posterior basal heptagonal. Radials 5, pentagonal; radial facet angustary. Three anal plates in cup; radianal pentagonal, proximal and left of C radial, isolated from anal sac; anal X pentagonal; anal sac not available. Arms of thick brachials, with U-sectioned ventral groove. Stem circular in section, strongly heteromorphic with alternating nodals and internodals of markedly different diameters, with rounded latus.

REMARKS. This material is preserved in medium to coarse sandstone, indicative of a higher energy environment than most Bokkeveld echinoderms which occur in the intervening shales. The two available slabs suggest considerable postmortem movement with most arms and stems disarticulated. However, no disarticulated cups are evident suggesting strong interplate sutures and/or cup shape less susceptible to disaggregation.

Family LECYTHOCRINIDAE Kirk,1934

**Othozecrinus** gen. nov.

TYPE SPECIES. *Othozecrinus royi* sp. nov.

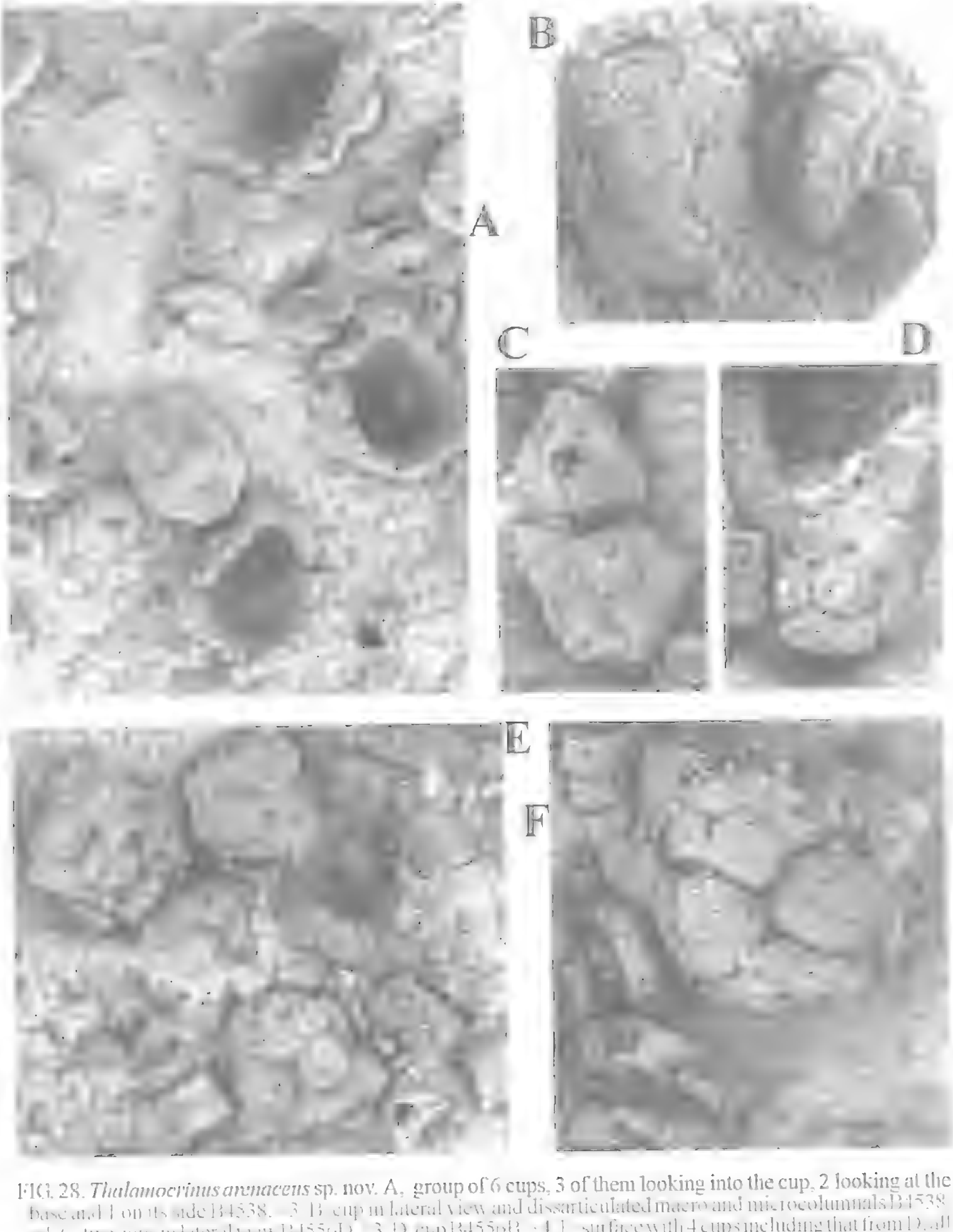



FIG. 28. *Thalamocrinus arenaceus* sp. nov. A, group of 6 cups, 3 of them looking into the cup, 2 looking at the base and 1 on its side B4538, ×3. B, cup in lateral view and dissarticulated macro and microcolumnals B4538, ×4. C, two cups in lateral view B4556D, ×3. D, cup B4556B, ×4. E, surface with 4 cups including that from D, all in lateral view B4556A, ×4. F, holotype crown showing posterior anal plates and part of an arm B4556C, ×5.

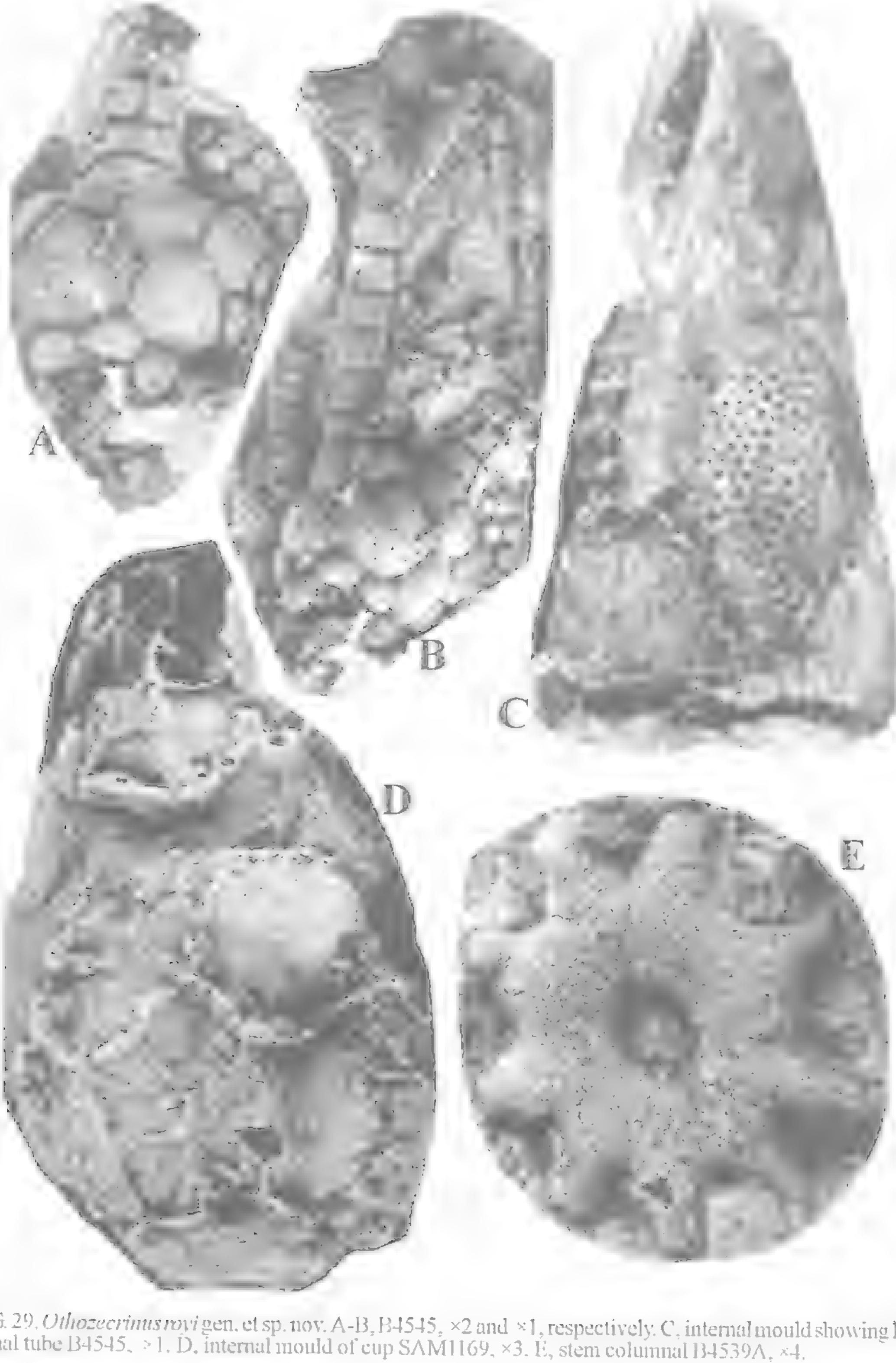



FIG. 29. *Othozecrinus royi* gen. et sp. nov. A-B, B4545, ×2 and ×1, respectively. C, internal mould showing large anal tube B4545, ×1. D, internal mould of cup SAM1169, ×3. E, stem columnal B4539A, ×4.

ETYMOLOGY. For Roy Oosthuizen, who collected much of the material described herein; an anagram to which is added only the 'cr'.

DIAGNOSIS. Cup wide bowl-shaped, with strongly convex plates; 5 infrabasals; radianal and anal X in cup in radial circlet. Anal sac of moderate length, inflated, of numerous large polygonal plates. Arms uniserial, branching isotomously; primibrach 7 axillary. Stem circular, relatively small diameter, with greatly expanded epifacet into 6-9 blunt spines.

REMARKS. While the details of this species are not entirely available, in particular the oral area and the branching pattern of the arms, it is sufficiently known to be confident it does not fit an existing genus. The two similarly sized (but differently shaped anal plates in the cup, convex infrabasals, 7 primibrachs and very distinctive stem combine to isolate this species. The Lecythocrinidae has members with 2 anal plates in the radial circlet. The anal plate arrangement of *Othozecrinus* is most similar (though not closely) to that of *Lecythocrinus* (cf Moore *et al.*,1978, fig.375.7) but the concealed infrabasals and the subquadrangular stem with large axial and 4 peripheral canals make close relationship unlikely. Other members of the family, *Cestocrinus* and *Corynecrinus*, have 0 or 5 anal plates in the cup and *Corynecrinus* has infrabasals concealed by the stem. The Euspirocrinidae is distinguished by its 3 anal plates in the cup and the Barycrinidae has a small radianal proximal to C radial. If forced to place this genus, with such distinctive stem, into a family it has to be the Lecytho- crinidae but that is a tentative assignment.

**Othozecrinus royi** gen. et sp. nov.
(Figs 29-31)

MATERIAL. HOLOTYPE: B4545 from Hex River Pass (C2S1, Gydo Formation). PARATYPES: SAM1169 from Boschluis Kloof (Gydo Formation), SAMK965 from Wolfaardt's Farm, Riet Valley, Ceres, B4524, B4539 from Grootrivier Hoogte (C2Q1, Gamka Formation), ROC20 Gamkapoort, Prince Albert at 33°18'S, 21°38'E (1st shale), ROL70 Warmwatersberg, Barrydale at 33°46'30"S, 20°55'30"E (1st shale). SUGD300 from De Dooms.B4600 from Platfontein in the Gydo Formation.

DIAGNOSIS. As for genus.

FIG. 30. *Othozecrinus royi* gen. et sp. nov., sketch of plate arrangement with arm branching as far as known on right and dotted lines on infrabasals indicating extent of stem facet. IB = infrabasal; B = basal; R = radial; RA = radianal; X = anal X; A-E above radials indicate rays.

DESCRIPTION. Cup short, wide bowl-shaped, of thick, strongly convex plates. Infrabasals 5, forming pentagonal circlet, strongly convex, with short strong almost spinose projections on A, B and C infrabasals in larger specimens; stem facet central, hemispherical concavity, depressed distal to projecting convexity of infrabasals, with distinct rim. Basals 5, smooth, convex with sutures depressed, hexagonal (but with 2 proximal sides at very high obtuse angle) except heptagonal CD and BC basals. Radials 5, convex, with 1st primibrach narrower than radial; articulating facet slightly declined outwards, with strong transverse ridge and distinct muscle and ligament areas. CD basal supporting 2 anal plates, with right just proximal to left; distal edges of these 2 plates level with distal margin of radial circlet. Anal sac short, squat; polygonal plating apparently irregularly arranged, with finely scalloped edge to each plate indicating perforate wall, perforations circular along sutures. Arms uniserial, thick, of long brachials, with sharp deep ambulacral groove; primibrach 7 axillary; rest of arms unknown. Stem of large columnals (c. 15mm across not including blunt lateral spines), up to 4mm long, with small (up to 4mm diameter) central circular articulum, with up to 10 large blunt lateral spines. Articulum with small central lumen showing 5 rounded pits, one at each corner of the pentagon and circular jugulum centrally; rest of articulum with radial ridges and intervening grooves forming triangular segments, with fine peripheral rim to articulum. Latus (epifacet) with smooth gently convex (in radial direction) surface, extended into stout blunt spines; 6-9 blunt spines per

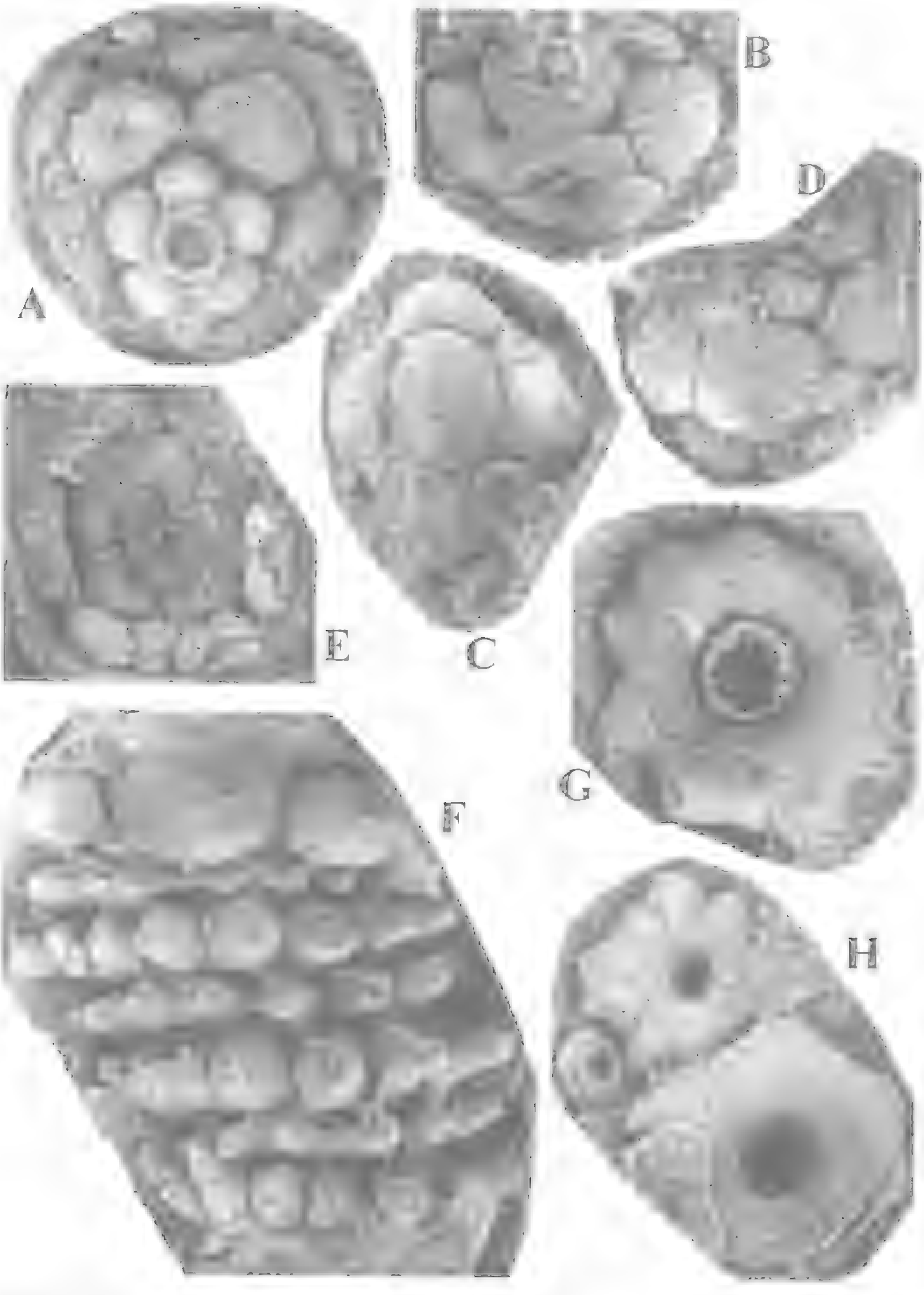



FIG. 31. *Othozecrinus royi* gen. et sp. nov. A, base of cup geol surv B4600, ×3. B, base of cup B4524, ×3. C, base of cup RO L70, ×3. D, lateral view of different cup RO L70, ×3. E, oral view of interior of cup SUGD300C, ×2. F, basal circlet with stem attached RO C20, ×3. G, columnal B4539B, ×5. H, columnals SUGD300A, ×3.

columnal. Blunt spines on every visible columnal in lateral view.

REMARKS. *Hyperexochus immodicus* Moore & Jeffords, 1968 from the Early Devonian of Tennessee has many lateral spines on its columnals and a small articulum but the surface of the articulum is differently ornamented and the spines are not in a single whorl, shaped differently and more numerous. *Sumaricystis radiatus* Stukalina, 1978 from the Middle Ordovician of the southern Tien Shan in central Asia is the most similar columnal but it has many more lateral spines and a narrow peripheral crenularium on the articulum. *Floricolumnus* Donovan & Clark, 1992 is similar in its greatly expanded epifacets which are almost spinose but in that genus they are well-separated nodals with smaller columnals between whereas in *Othozecrinus* they occur on each columnal evident (Fig. 31F). However, the central depression and narrow crenularium on both sides of these columnals indicate that at least one unexpanded columnal occurs between every pair of expanded ones. It seems unlikely that any of these genera is closely related to *Othozecrinus* and that the columnals with expanded epifacets have evolved independently in each case.

## Class ASTEROIDEA
## de Blainville, 1830

Terminology and suprageneric classification largely follow Spencer & Wright (1966) except that: 1) their 'Mouth angle plate' (MAP) (='oral ossicles' of Blake & Guensburg, 1989) is here termed 1st ambulacral plate (AMB1) following Smith & Jell (1990); 2) their Amb1 is here termed ambulacral 2 following Bjork et al. (1968) and Smith & Jell (1990); 3) 'dorsal' and 'ventral' are used both for body and ossicle surfaces; 'adradial' and 'abradial' for directions toward and away from the arm axis, respectively; and 'proximal' and 'distal' for directions toward and away from the mouth, respectively. Dimensions of plates in the arms are indicated by: (rad.) = in radial direction or length of arm; (ad.-ab.) = in adradial-abradial direction across arm. In general, dimensions are referred to as 'long' and 'short' in the radial direction and 'wide' or 'narrow' across the arm.

### Family PROMOPALAEASTERIDAE
### Schuchert, 1914

### **Aulacolatiaster** gen. nov.

TYPE SPECIES. *Aulacolatiaster breviramus* sp. nov.

ETYMOLOGY. Latin *aulax*, furrow, *latus*, wide and *aster*, a star, referring to the wide ambulacral groove.

DIAGNOSIS. Arms 5, short (no longer than diameter of disc), wide. Dorsal surface with primary ossicular ring of large ossicles centrally. Ventral surface dominated by wide elliptical ambulacral grooves; ambulacrals wide, opposite, with extremely shallow ambulacral channel, with fine parallel ambulacral ridges running abradially parallel to plate margins and separating podial basins; 1st ambulacrals large, oriented vertically, paired across interradii; inferomarginals with pair of short lateral spines, becoming elongate proximally, isolating from the margin of the frame at least 1 narrow axillary (odontophore) in each interradius; adambulacrals with transverse row of extremely large prominent tubercles.

REMARKS. This genus is distinctive in its combination of meshwork dorsal plating in distinct radial columns, wide ambulacral groove with wide ambulacrals bearing fine parallel ridges separating podial basins, adambulacrals with row (ad.-ab.) of very large prominent tubercles and inferomarginals becoming wider proximally and each with 2 lateral spines. We consider it most closely allied to *Promopalaeaster* Schuchert, 1914 with which it shares the same type of dorsal plating, wide ambulacral groove, large 1st ambulacral, and interradial structure but from which it may be distinguished by its parallel ambulacral ridges indicating a single column of tube feet along each side of the arm, extreme size of the tubercules in a transverse row on the adambulacrals and short arms which could prove to be growth related when more material becomes available. Ambulacral ridge structure proximally distinguishes North American species, including the type species of *Promopalaeaster* but *Promopalaeaster elizae* Spencer, 1930 from the Upper Ordovician of Scotland and *Eoactis simplex* Spencer, 1914 from the Lower Silurian both exhibit (Spencer & Wright, 1966, figs 50.1 and 50.2c) ambulacral ridges parallel to each other and to the interplate sutures throughout as in *Aulacolatiaster*.

*Aulacolatiaster* bears some resemblance to *Palasterina* McCoy, 1851 in the wide ambulacral groove, parallel ambulacral ridges, and large 1st ambulacrals but is distinguished by its interradial structure and dorsal plating. Its placement will remain problematic until better preserved

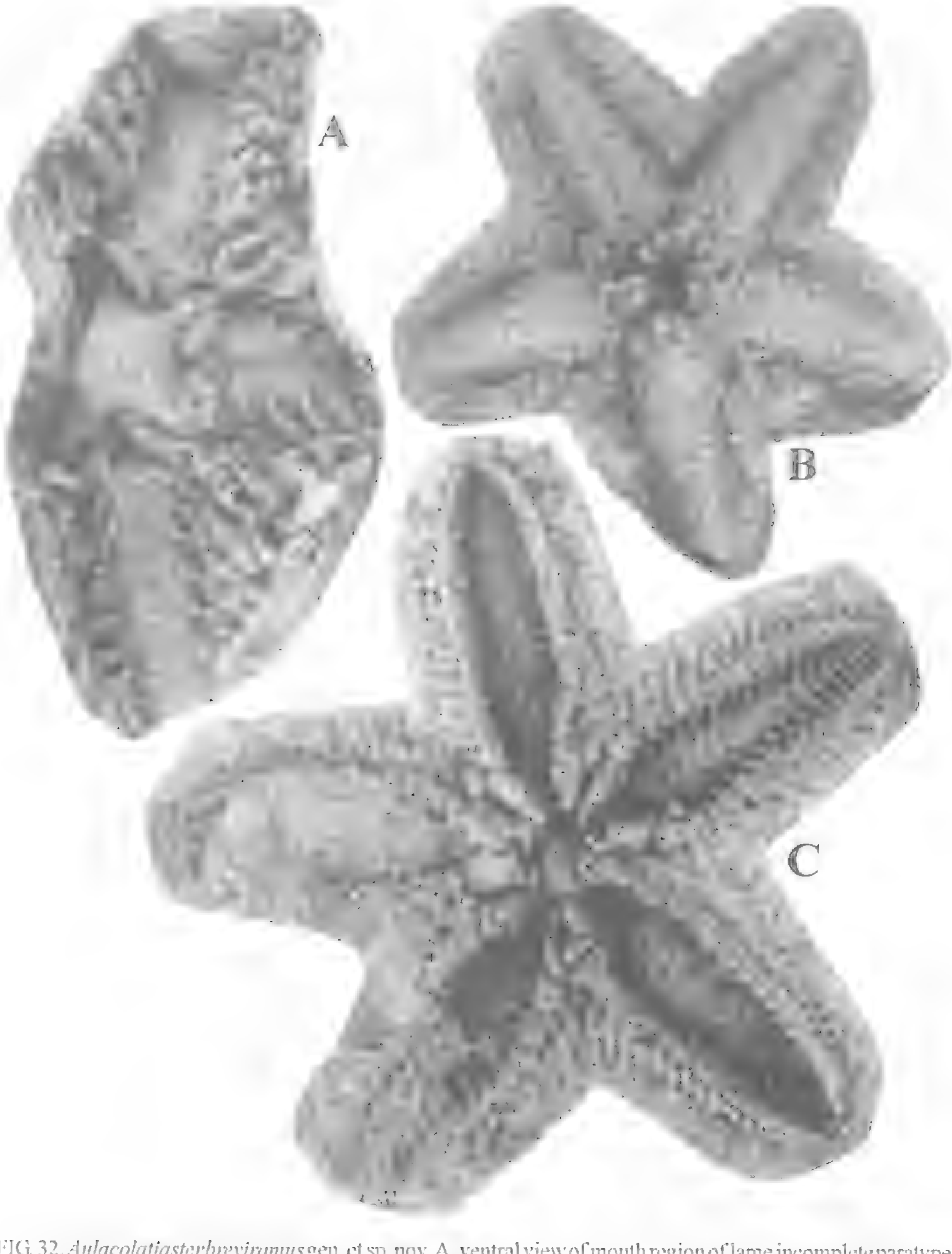



FIG. 32. *Aulacolatiaster breviramus* gen. et sp. nov. A, ventral view of mouth region of large incomplete paratype with mouth wide open SAMK1063, ×4. B-C, dorsal and ventral views, respectively, of holotype SAMK1018a & b, ×4 and ×6, respectively.

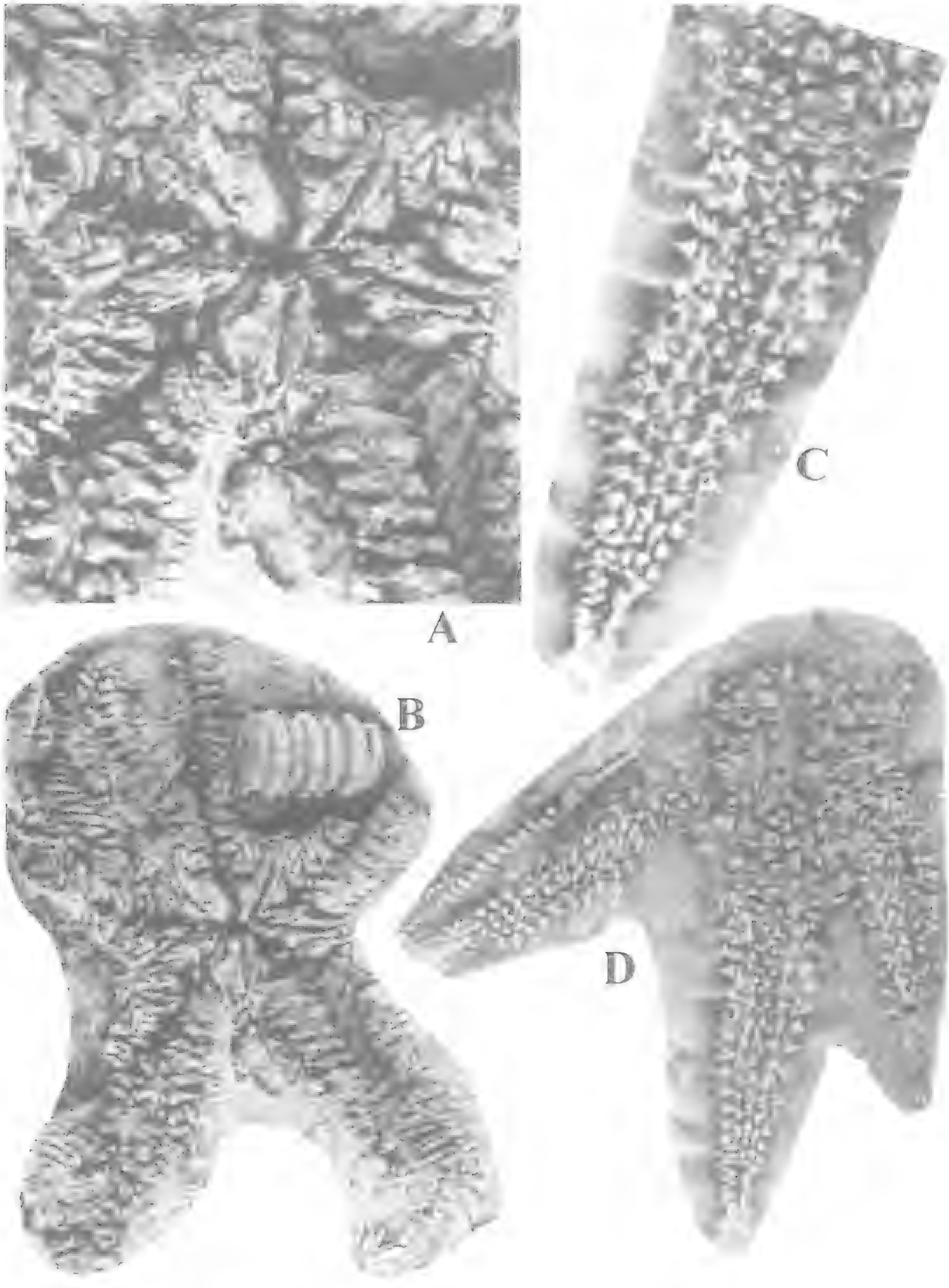



FIG. 33. *Ulrichaster macrodentatus* sp. nov. A-B, enlarged ventral view of oral region and ventral view of incomplete paratype with short section of crinoid stem in upper right RO 44, ×6 and ×3, respectively. C-D, enlarged dorsal view of arm and dorsal view of incomplete holotype PRV725, ×6 and ×4, respectively.

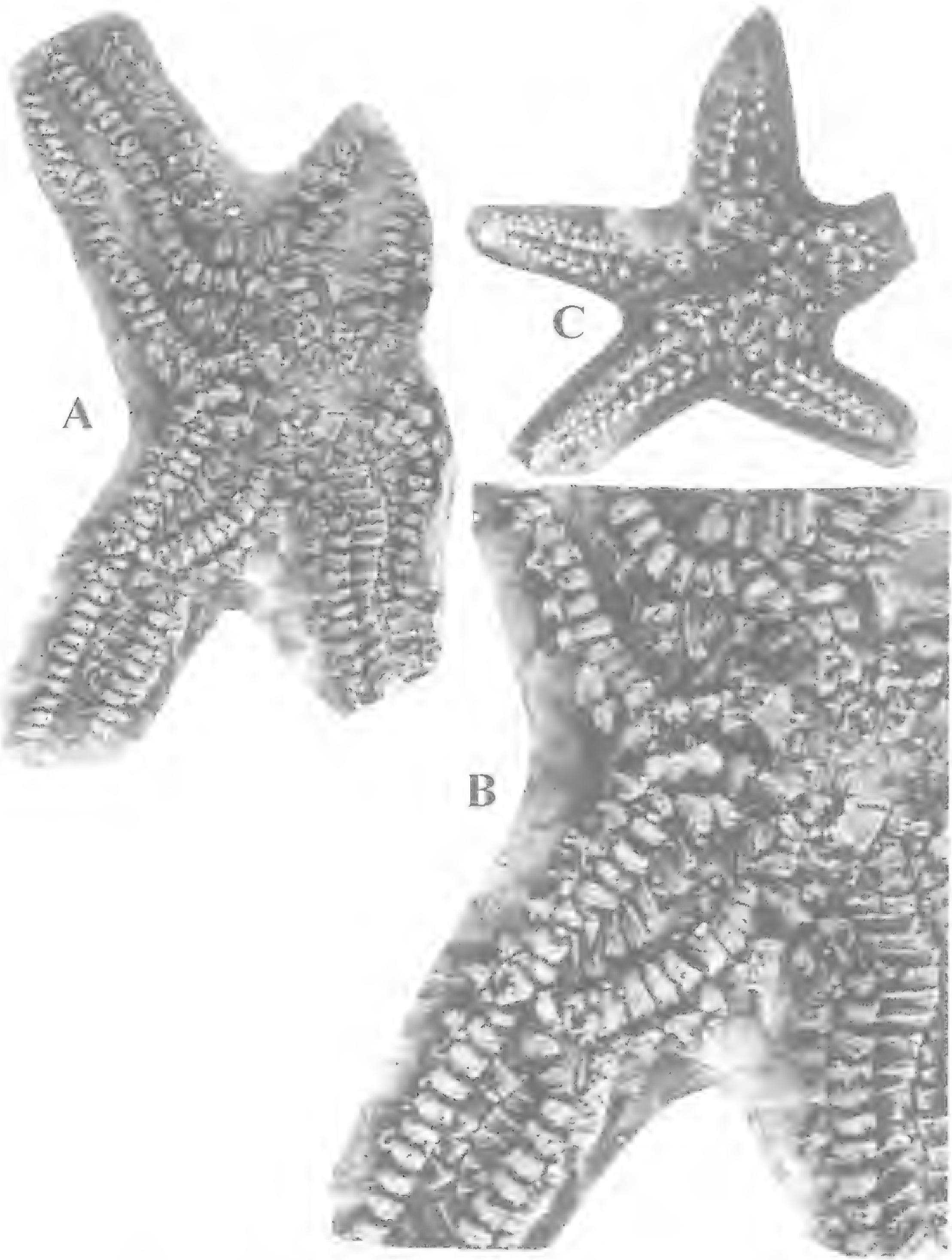



FIG. 34. *Ulrichaster macrodentatus* sp. nov. A-B, ventral view of slightly disarticulated paratype and enlargement of its oral area PRV737, ×5 and ×8, respectively. C, juvenile paratype in dorsal view PRV738, ×10.

material becomes available, particularly a dorsal surface.

**Aulacolatiaster breviramus** sp. nov.
(Fig. 32)

ETYMOLOGY. Latin *brevis*, short and *ramus*, arm; for the relatively short arms.

MATERIAL. HOLOTYPE: SAMK1018, dorsal and ventral external moulds from Riet River, N of Ceres Division on Wupperthal Road; S side of farm which is also called Groot Rivier in the neighbourhood; Gydo Fmn, 33m below top of unit; SAMK1063 incomplete ventral external mould from Wolfaardt's Farm near Ceres, about 100m NNE of the house.

DIAGNOSIS. As for genus.

DESCRIPTION. Stellate. Arms 5, short (10mm from oral axis to arm tip on holotype), wide (4mm at widest point). Dorsal surface with primary ossicular ring of large ossicles in radial positions and with central pit or perforation on each, outlines unclear but apparently subquadrate; a further circlet of large ossicles probably present in interradial positions and resting on the circlet of radially disposed ossicles (single dislocated subrectangular plate lying in interradial position (Fig. 32B); dorsal surface of arms with broad median groove (probably preservational), with midline bordered by columns of weakly tuberculate plates that abut along the midline of the arm, with at least 3 columns of tuberculate plates abradially separated by deep pits (suggesting some sort of meshwork stucture but this remains unclear from the available specimen), with columns of plates laterally aligned into rows across the arm, without clearly defined superomarginals. Ventral surface with small interradii and wide elliptical arms; ambulacral grooves elliptical, occupying about 2/3 arm width for most of arm length (more than 80% distally), extending to arm tip; ambulacrals wide, opposite, with extremely shallow median ambulacral channel; ambulacral ridges fine, parallel, with very small expansion at adradial end, running abradially parallel to plate sutures (this attitude not absolutely certain but where sutures between successive ambulacrals are evident they are parallel to the ridge), weakly expanded at abradial end to about same length as adambulacral; 1st ambulacrals large, plough shear-shaped, oriented vertically, paired with convex sides adjacent across interradii; inferomarginals wider than long, becoming much wider proximally with at least 1 axillary (and possibly 3 or 4) separating adambulacrals from inferomarginals in each interradius, with pair of short lateral spines directed abradially on each inferomarginal; adambulacrals with transverse row of prominent tubercles (tubercles may be irregularly arranged in smaller individual but well aligned in transverse rows from expanded abradial end of ambulacrals in large individual (Fig. 32A))

REMARKS. The holotype is known from external moulds of both surfaces but whereas the ventral mould is very well preserved the dorsal mould seems to have been abraded (probably since collection) and does not preserve much detail. The fragmentary external mould of the ventral oral area of a larger individual is well preserved but only a small fragment. Both casts of the ventral surface have a convex mound of matrix in the oral pole suggesting that the central dorsal structure was weak and collapsed easily upon death. Well-developed podial basins between the ambulacral ridges abradially are shared by contiguous ambulacrals but preservation is not good enough to determine whether or not a pore passes through the basin floor.

Family URASTERELLIDAE Schuchert, 1915

**Ulrichaster** Spencer, 1950b

TYPE SPECIES. *Urasterella ulrichi* Schuchert, 1915 from the Middle Ordovician of central USA.

REMARKS. Spencer (1950b) subdivided *Urasterella* McCoy into a group with a single row of ossicles in the dorsal midradius of the arms (further subdivided on features of dorsal arm ossicles between the radial and marginal columns) and a second group with 2 rows of ossicles in the dorsal midradius (i.e., on either side of the arm axis). He erected *Ulrichaster* for the latter group which accepts the new species described herein.

**Ulrichaster macrodentatus** sp. nov.
(Figs 33, 34)

ETYMOLOGY. Greek *macros*, long and *dentatus*, tooth; for the long 1st ambulacrals.

MATERIAL. RO44 from the Voorstehoek Shale (C2S2) at 33°30'S; 19°49'E near Matroosberg, Worcester (Hex River Pass). PRV738, 737 (and counterpart PRV725) from Tafelberg in the Waboomberg Shale (C2S4).

DIAGNOSIS. Dorsal surface with very open meshwork of ossicles in radial columns, columns symmetrical about arm axis. 1st ambulacrals large, elongate, reaching interradial margin or

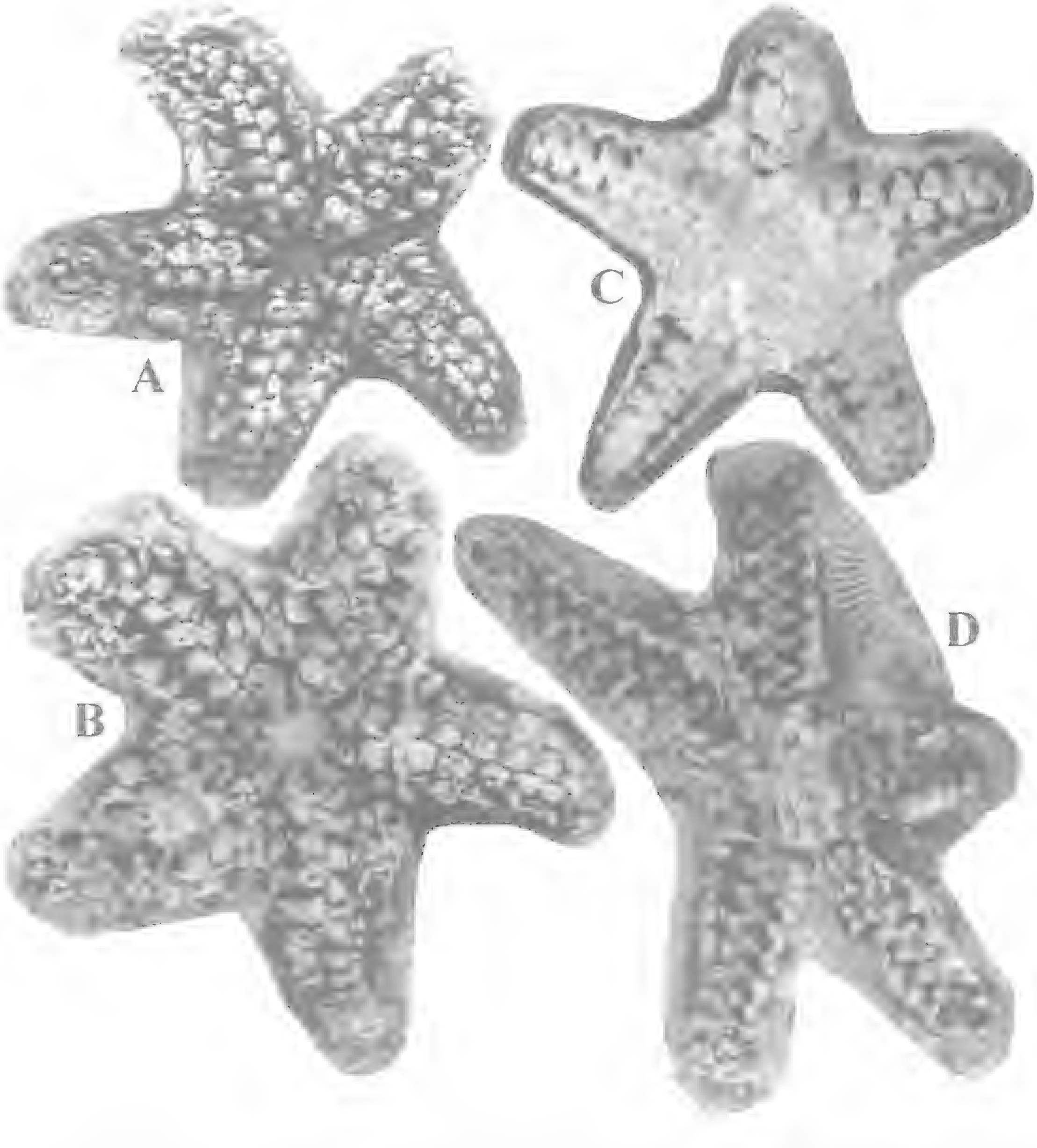


FIG. 35. *Haughtonaster reedi* Rilett, 1971. A-B, ventral and dorsal views of juvenile holotype SAM 3881, ×5. C, dorsal view of juvenile paratype SAM3375, ×5. D, ventral view of SAM K978, ×6.

close to it, in closely adjacent pairs across interradii.

DESCRIPTION. Stellate. Arms 5, long (at least twice disc diameter). Dorsal surface an ordered meshwork (with large perforations) of small tuberculate elongate plates in 4 radial columns (2 columns on either side of arm axis smaller than next columns abradially) linked by less regular struts in transverse rows, without obviously differentiated primary ossicular ring or other plates (but disc plating not clear on available specimens). Ventral surface with long parallel sided ambulacral grooves; ambulacrals wide, opposite, with diagonal ambulacral ridges having curved ventral edges forming basins abradially.

1st ambulacrals large, extending to interradial margin, straight but with strong lateral projection on adradial side, paired across interradii; adambulacrals narrow, subrectangular to subdiscoidal in ventral view, without spines; inferomarginals forming lateral margins of arms, small (same size as abradial dorsal plates), with 1 or 2 or more short stubby spines forming spinose margin.

REMARKS. None of the available material is well preserved but enough is available to show the features of *Ulrichaster* in particular the short stubby spines of the inferomarginals and abradial dorsal plates and the ordered meshwork of radial columns of the dorsal plating with 2 columns either side of the arm axis. However, shape of the 1st ambulacrals and the larger pits between dorsal plates distinguish it from other members of the genus. The type species, *U. ulrichi* has more columns of ossicles covering the arm dorsally and does not appear to have the larger pits of the dorsal meshwork as in *U. macrodentatus*. *U. gutterfordensis* Spencer, 1918 has small 1st ambulacral plates. *Salteraster biradialis* Withers & Keble, 1934 from the Ludlow of Victoria (included by Spencer (1950b) in *Ulrichaster*) is an ophiuroid with the 2 median rows of ossicles the dorsal side of the ambulacrals, any dorsal plating having been removed or not preserved.

Class OPHIUROIDEA Gray, 1840
Order STENURIDA Spencer,1951
Suborder PAROPHIURINA Jaekel, 1923
Family EOPHIURIDAE Schöndorf, 1910

**Haughtonaster** Rilett, 1971

TYPE SPECIES. *Haughtonaster reedi* Rilett, 1971 from the Gydo Formation near Ceres.

DIAGNOSIS. Disc pentagonal, dorsal surface of smooth oval plates surrounded by an irregular mass of very fine, almost spicular elements; ventral interradii triangular, with polygonal plates having some perforations on sutures (i.e. a few oppositely scalloped margins of plates). Ambulacrals offset across arm axis, rectangular in dorsal view; adambulacrals wide and gently oblique to arm axis in ventral view, forming lateral walls of arm; podial basins subcircular, very deep. 1st ambulacral with strong curved ridge forming distinctive elliptical basins interradially.

REMARKS. Rilett (1971) assigned this genus to the Eophiuridae to which Spencer & Wright (1966) assigned only *Eophiura* from the Arenig of Czechoslovakia. The more mature specimens now available indicate that a close relationship is unlikely although the 2 genera should probably be retained in the same suborder. Hotchkiss (1976) established a subordinal level division of the Stenurida based on whether ambulacrals were opposite or offset across the arm axis, noting that pre-existing classification had been based on grades of development and inferring that the development of offset ambulacral columns indicates a monophyletic clade of Palaeozoic ophiuroids. He erected the Scalarina for stenurids with opposite ambulacrals and the Parophiurina is available for those with offset ambulacrals. Phylogeny within the Paraophiurina is not clear and would require a review of known members, which is outside the scope of this paper. *Haughtonaster* is distinctive in that suborder in lacking spines on the arms, lacking a column of sublateral plates, in its long slender tapering arms, in its deep circular podial basins and in its wide adambulacrals enclosing the arm laterally. In the shape of ambulacrals along each arm, nature of adambulacrals and podial basins, and in particular the distinctive ridge on the 1st ambulacral, *Haughtonaster* very much resembles *Stenaster* Billings, 1858. However, that genus belongs to the Scalarina and a close relationship would not be possible unless the offset arrangement of ambulacrals evolved more than once. We do not speculate on that possibility and retain *Haughtonaster* in the Parophiurina. Because we can see no workable family arrangement we retain Rilett's (1971) family assignment.

**Haughtonaster reedi** Rilett, 1971
(Figs 35-37)

MATERIAL. HOLOTYPE: SAM3881 from Hottentots Kraal. PARATYPE: SAM3375 from Hottentots Kloof, Ceres. OTHER MATERIAL: ROC50, RO122, RO804 from Gamkapoort, Prince Albert at 33°18'S, 21°38'E in the Gydo Formation; B4567 from Swaarmoed Pass, 1.3 miles from Great Swaarmoed Farm, Ceres; PRV1484, SAM13472 from Voetjies Kloof Suid; SAM13470; SAMK1016 from Riet River (also called Groote Rivier) N of Ceres Division on Wupperthal Road, S side of farm in Gydo Formation; SAMK978 from Wolfaardt's Farm near Ceres (100m NNE of house).

DESCRIPTION. *Overall form*. Maximum radius 7-30mm, disc radius 5-6mm. Arms 5, short and blunt in small specimens, in large specimens weakly petaloid in proximal 1/2 and strongly tapered over distal 1/2, with elongate pointed tip. Disc pentagonal, extending to 5th or 6th

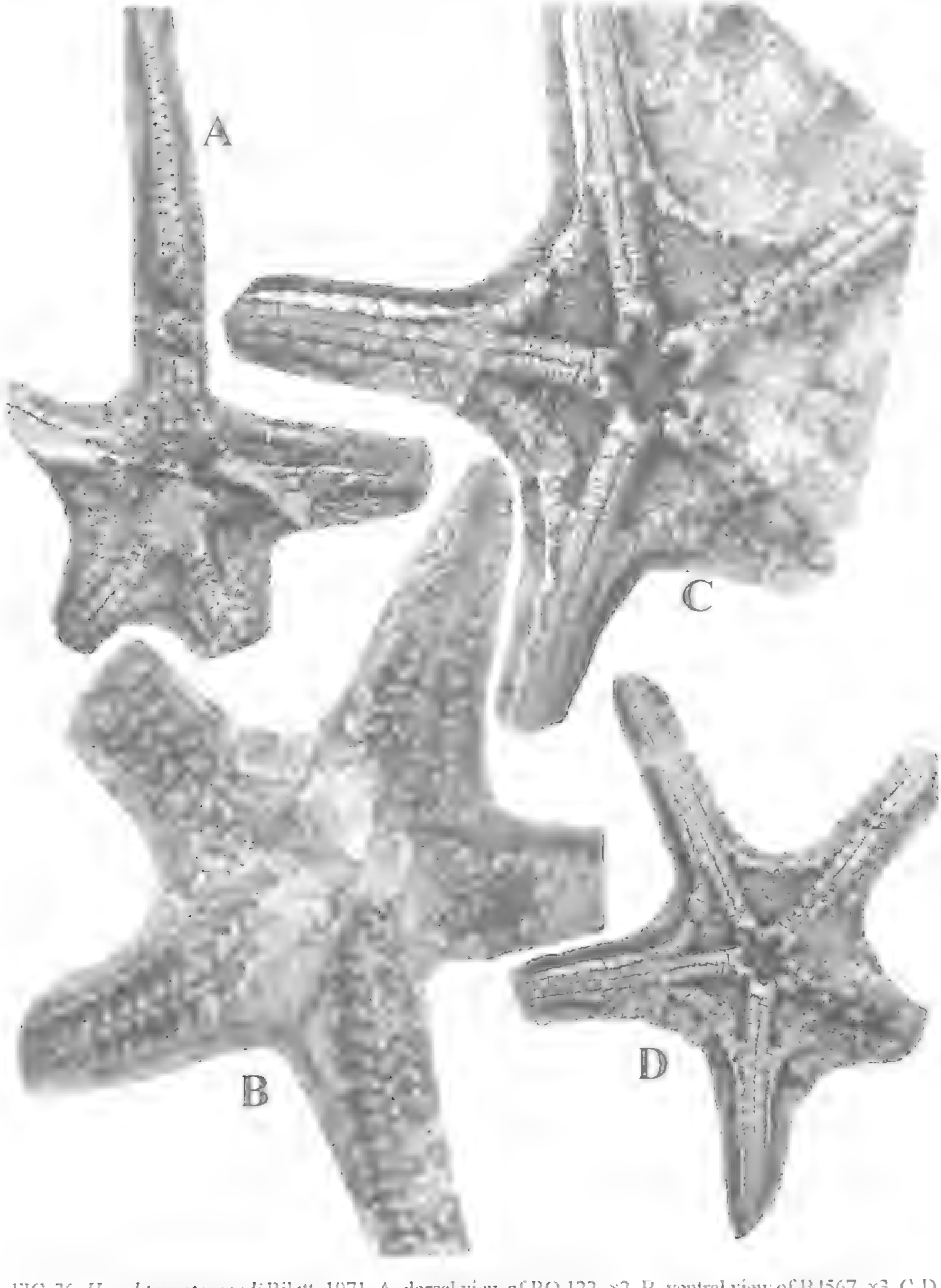



FIG. 36. *Haughtonaster reedi* Rilett, 1971. A, dorsal view of RO 122, ×2. B, ventral view of B4567, ×3. C-D, dorsal views of RO C50, ×4 and ×2, respectively.

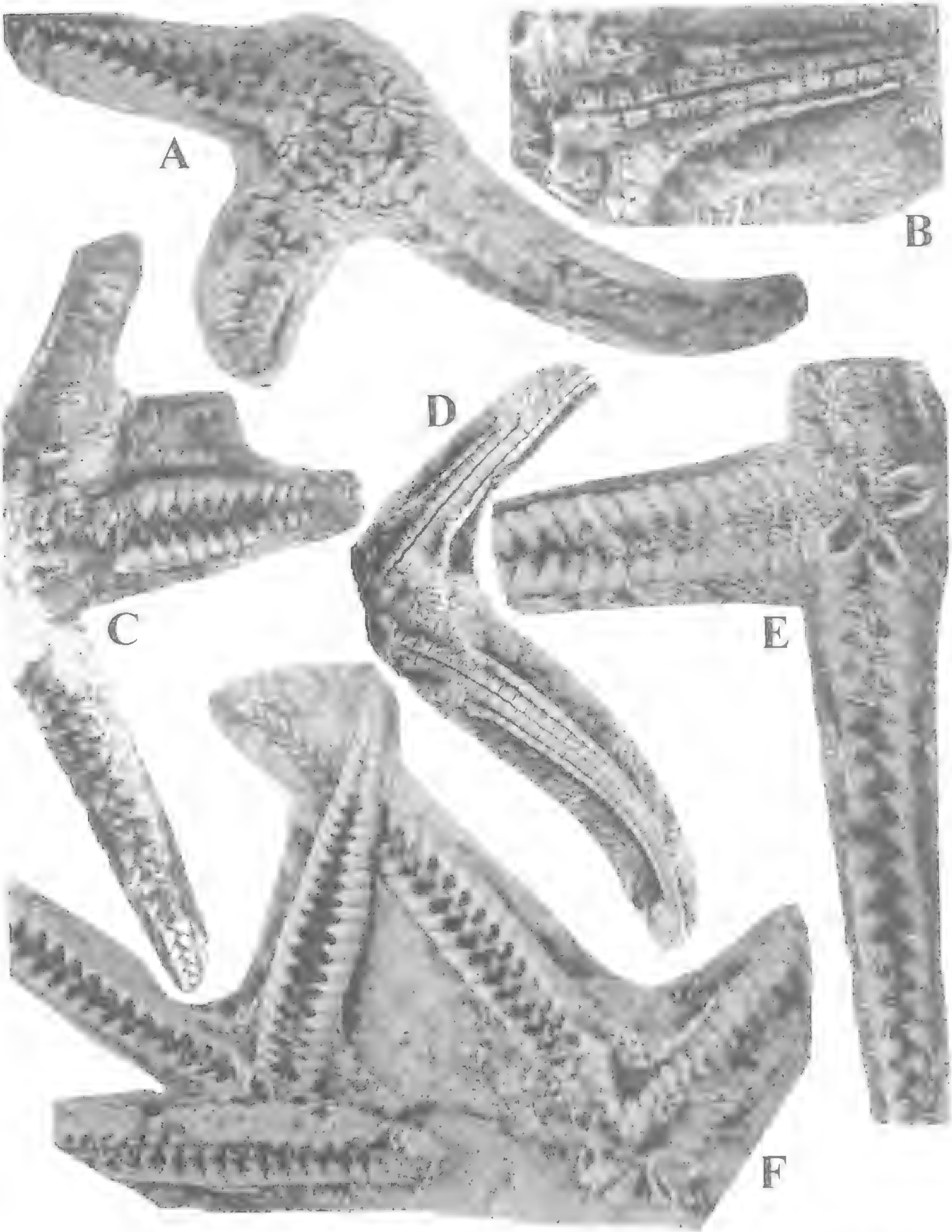



FIG 37. *Haughtonasterreedi* Rilett, 1971. A, ventral view of incomplete smaller specimen RO 804, ×6. B, dorsal view of proximal part of arm RO C50 ×4. C, ventral view of incomplete adult SAM13472 ×3. D, dorsal view of incomplete adult RO C50 ×2. E, ventral view of incomplete adult SAM13470 ×4. F, ventral view of 2 adults PRV 1484 ×4.

ambulacral; in small specimens only 3-4 tiny plates in interradius, in larger specimens 8-12 polygonal plates in a triangular interradius, plates irregularly polygonal, possibly disc plates with scalloped margins in larger specimens (no area of plating well preserved). Only small fragments of dorsal disc available.

*Arm plating.* Ambulacrals in dorsal view subquadrate (in smaller specimens) to subrectangular (larger specimens), offset across arm axis distal from 2nd ambulacral, with sharp elliptical clefts between successive ambulacrals in each column, with weakly zigzag (obtuse projection at midlength of ambulacrals pointing at recessive interambulacral suture in opposite column of ambulacrals) line of suture between the 2 columns in arm axis. Ambulacrals in ventral view subtrapezoidal, separated from succeeding ambulacral in same column by shallow rounded basin shared by 2 ambulacrals (i.e. interambulacral suture runs through middle of depression) and descending abradially into deeper part of podial basin, with straight radial axis between 2 ambulacral columns; ambulacral channel very shallow, barely discernible. Adambulacrals in dorsal view subtriangular, extending ventrally to form the abradial wall of the arm, with adradial tip directed at proximal end of ambulacral. Adambulacrals in ventral view wide, with parallel interadambulacral sutures, continuing abradially to form lateral wall of arm, without spines, with sharp adradial projection between podial basins. Podial basins subcircular with slight expansion on adradial side between adjacent ambulacrals, extremely deep adjacent to adambulacrals and shallower adjacent to radial axis of arm, apparently with some subtle ledges and dimples on the evenly curved walls (but preservation is not good enough to be certain of consistent structures).

*Mouth frame.* Dorsal aspect not available except in small specimen; central circular dorsal depression but plating details not available. Mouth small; no buccal slit. Smallest specimen with 1st ambulacral unspecialised except for slight proximal projection. 1st ambulacral becoming more elongate (radially) with growth, developing strong curved ridge convex towards arm axis; curved ridges from adjacent arms forming distinctive elliptical basins interradially.

REMARKS. The marked changes that take place in this species during growth involving increasing arm length relative to width and development of the pentagonal disc could be considered indicative of separate species if it were not for the distinctive structure of the 1st ambulacrals and the broad adambulacrals forming the lateral walls of the arms that link the specimens over the whole size range. There is no discernible variation in the available material of the same size. As discussed under the generic remarks above the only species deserving of comparison is *Stenaster obtusus*, which has its ambulacrals opposite each other.

**Ophiuroid arm** indet. A
(Fig. 58A)

MATERIAL. SAMK625 from Gamkapoort.

DESCRIPTION. This specimen, preserved only as an external mould, is interpreted as the ventral aspect of a part of a free arm with the 2 alternating columns of vaguely hexagonal ambulacrals on the right, serving to identify the slightly zigzag arm axis; proximal is inferred as up the page from the gradually diminishing size of plates in the opposite direction (distal); a column of transverse plates abutting the ambulacrals laterally is interpreted as a column of sublaterals; the column of longitudinally elongate plates forming the lateral margin of the arm (and to which the abradial end of the sublaterals abut at the junction between successive plates) is interpreted as the lateral column and is not obviously spinose. The subquadrate depressed areas bordered by the ambulacral and lateral columns and separated by the sublaterals (podial basins?) are fully floored and have 2 distinct depressions on that floor; one is adjacent to the distal end of the ambulacral and the other is proximal and abradial against the lateral plate.

REMARKS. Structure of the arm with 3 columns of plates (ambulacrals, sublaterals and laterals) suggests a primitive ophiuroid among the Stenurida (cf. *Eophiura*, *Pradesura*, *Stuertzaster* etc.). The alternating columns of ambulacrals exclude it from Hotchkiss's (1976) Scalarina and place it in the Parophiurina as used herein. However, there is no comparable form in this or any related group. Other stenurids with alternating ambulacrals may have the podial basin entirely on the ambulacrals (*Eophiura*, *Pradesura*) or have very wide podial basins (*Stuertzaster*) but none have the subquadrate podial basins of this South African form. This specimen represents a new genus but provides insufficient information for its definition forcing us to retain it in open nomenclature. The position of the sublaterals forming the proximal margin of

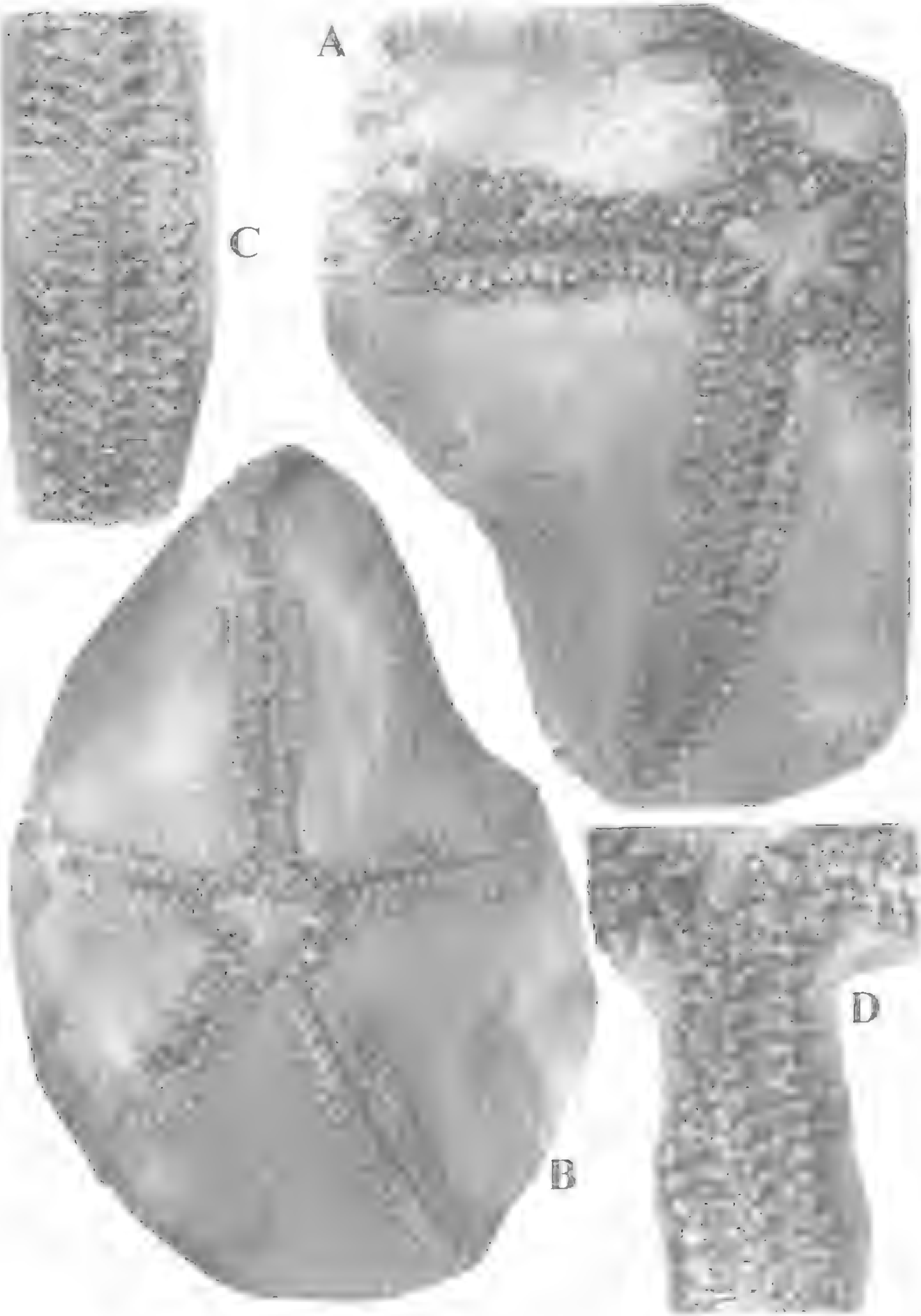



FIG. 38. *Hexuraster weitzi* (Spencer, 1950a), lectotype, SAM11055. A, ventral view (mould and thus latex cast incomplete) ×1.5. B, dorsal vie ×0.9. C-D, enlargements of parts of arms from A in ventral vie ×2.5.

the podial basin suggests a possible affinity with *Stuertzaster*, which is as much as can be said at the moment.

Order OEGOPHIURIDA Matsumoto, 1915
Suborder LYSOPHIURINA Gregory, 1896
Family CHEIROPTERASTERIDAE Spencer, 1934

**Hexuraster** gen. nov.

not *Hexura* Simon, 1884: 314.
*Hexura* Spencer, 1950a: 300.

TYPE SPECIES. *Hexura weitzi* Spencer, 1950a from the Lower Devonian of South Africa.

DIAGNOSIS. Body large (incomplete holotype 130x80mm); disc uncalcified, extending to arm tips. Arms slightly petaloid. Ambulacrals cylindrical with lateral projection (or toe of boot) shorter than radial length. Adambulacrals wide (ad-ab), expanded abradially to be T-shaped, with single very strong lateral spine on each adambulacral. Madreporite interradial, close to mouth frame on ventral surface. Mouth frame small for size of animal, plates not massive, with well-developed podial basin on 2nd ambulacral. Mouth large, with short buccal slit between 1st 2 ambulacrals.

REMARKS. Spencer's (1950a) name was preoccupied by a spider genus so the replacement name is proposed herein. Spencer (1950a, figs 1 - 3 - 4) included 3 specimens which are assigned herein to 3 different genera. Jell (1997) chose SAM11055 (Spencer, 1950a, figs 1,2) as lectotype of *H. weitzi* and placed it in the Cheiropterasteridae which he reinstated from synonymy with the Encrinasteridae (Spencer & Wright, 1966). Spencer (1950a) allied *Hexuraster* with his Euzonosomatidae (=Encrinasteridae of Spencer & Wright, 1966) and although he quoted several reasons that do not apply to the lectotype of the type species but rather to his figs 4 and 5 we consider the Cheiropterasteridae closely related to the Encrinasteridae. Following Jell (1997), the family is known from the Early Devonian of Germany and South Africa and the Early Carboniferous of Indiana.

**Hexuraster weitzi** (Spencer, 1950a)
(Figs 38, 39)

*Hexura weitzi* Spencer, 1950a: 300, figs 1, 2 (not figs 3-5).

MATERIAL. LECTOTYPE: (chosen Jell, 1997) SAM11055 (130×80mm) from the Lower Devonian Bokkeveld Series, at De Dooms; RO45 (about 30mm diameter) from the Gydo Formation at Gamkapoort, Prince Albert, 33°18'S, 21°38'E.

DIAGNOSIS. As for genus.

DESCRIPTION. *Overall form.* 5-armed, preserved radius 15-65mm, arm radius just greater than disc radius. Arms slightly petaloid, with rounded only weakly tapered tips. Disc very large, uncalcified, extending to arm tips, with high obtuse angled re-entrant in some interradii but continuing almost circular in other interradii.

*Arm plating.* Ambulacrals subquadrate in dorsal view, offset across arm axis distal from ambulacral 3, boot-shaped in ventral view, with narrow cylindrical leg, long lateral process (foot) having a slight concavity on proximal side (instep) to receive abradial tip of distal end of next proximal ambulacral. Ambulacral channel prominent, formed by half grooves along the adradial edge of each ambulacral, with straight line of suture between 2 ambulacral columns in bottom of amulacral channel. Adambulacrals with long lateral projection abutting against the toe of ambulacrals; in dorsal view abradial subtrapezoidal expanded part of adambulacral with sharp proximal-distal ridge aligned on all adambulacrals to form ridge along the length of arm; ridge sharper on adradial side than on abradial side, with furrow on abradial side; lateral face subcircular to oval, flat, with single stout lateral spine attached apparently by suture. In ventral view expanded head of adambulacral subcircular, with low proximal-distal ridge aligned along the arm into one long ridge.

*Madreporite.* Subcircular to oval, large (4mm max. diameter in lectotype), possibly with vermiform ornament (not entirely clear in lectotype), situated only slightly asymmetrically interradially adjacent to ambulacral 2.

*Mouth frame.* Mouth very large in available specimens, with 1st ambulacral situated interradially leaving large embayments in each arm axis. 1st ambulacral long and narrow with deep transverse groove near midlength in dorsal view, similarly shaped but without transverse furrow in ventral view, with sutured junction to 2nd ambulacral almost radial. Smaller specimen with smooth basin-like recess under distal part of 1st ambulacral. 2nd ambulacral little different from more distal ambulacrals, subquadrate, indistinct in dorsal view, subquadrate, with well-developed podial basin in ventral view.

FIG. 39. *Hexuraster weitzi* (Spencer, 1950a), incomplete juvenile in ventral view RO 45 -4.

REMARKS. The lectotype has some iron oxide minerals deposited in the external mould obscuring details in some areas, particularly in the mouth frame but details of the arms are available by reference to different parts of the mould.

Family ENCRINASTERIDAE Schuchert, 1914

**Encrinaster** Haeckel, 1866

not *Aspidosoma* Fitzinger, 1843.
*Aspidosoma* Goldfuss, 1848: 145; Schöndorf, 1910: 4
*Encrinaster* Haeckel, 1866:67; Lehmann, 1957: 28; Spencer & Wright, 1966: U85
*Euzonosoma* Spencer, 1930: 411; Spencer & Wright, 1966: U86; Lehmann, 1957: 24

TYPE SPECIES. *Aspidosoma arnoldi* Goldfuss, 1848 from the Lower Devonian of Germany.

SPECIES ASSIGNED. *arnoldi*, *tischbeinianus*, *petaloides*, *eifelensis*, *goldfussi*, *pontis*, *roemeri*, *schmidti* and *laevidiscus*.

REMARKS. The several German species of this genus were reviewed by Schöndorf (1910) (as *Aspidosoma*) and Lehmann (1957). Spencer (1930) spread these German species and others from Britain and North America between *Encrinaster* and *Euzonosoma*. Generic placement of *tischbeinianus* depends on the concepts of these 2 genera.

Spencer (1930: 404) provided a key for genera of his Euzonosomatidae, a junior synonym of Schuchert's Encrinasteridae, in which he indicated the 'Geno-holotype' of *Euzonosoma* as *E. petaloides* (Simonovitsch). In the same work (1930: 411) he appears to have tried to designate a different genotype in the sentence '*Euzonosoma orbitoides*, n. sp., is chosen as the holotype of the species'. Although his intention is not clear from this work, the first of these citations links the words genus (geno-) and type (holotype) and must be accepted as a valid designation of a type species. The second citation does not link the words 'genus' and 'type' in any way and cannot be considered a valid designation of a genotype or type species. Therefore, the type species of *Euzonosoma* is *Aspidosoma petaloides* Simonovitsch, 1871 by original designation.

No action by any subsequent author can change this designation. Even subsequent action by the original author (e.g., Spencer & Wright, 1966) cannot supplant the original designation. So regardless of Spencer's intentions, which may be inferred from his subsequent citation of *E. orbitoides* as the type species and despite subsequent workers acceptance of *E. orbitoides* as type, *E. petaloides* must be considered the type species. This recognition should not greatly change the concept of *Euzonosoma* because Spencer (1930: 404) included that species in his generic concept.

Spencer (1930) distinguished between these 2 genera in his key by only 1 feature, the degree of widening (ad-ab) of the adambulacrals in the median regions (i.e., midlength) of the arm: in *Euzonosoma* the adambulacrals are distinctly broader in the median region than at the extremity whereas in *Encrinaster* adambulacrals are only slightly differentiated (inferring some widening but only slight) compared to the extremity. The variation usually comes down to width of the adambulacrals within the disc as opposed to their width just outside the disc. Most authors and

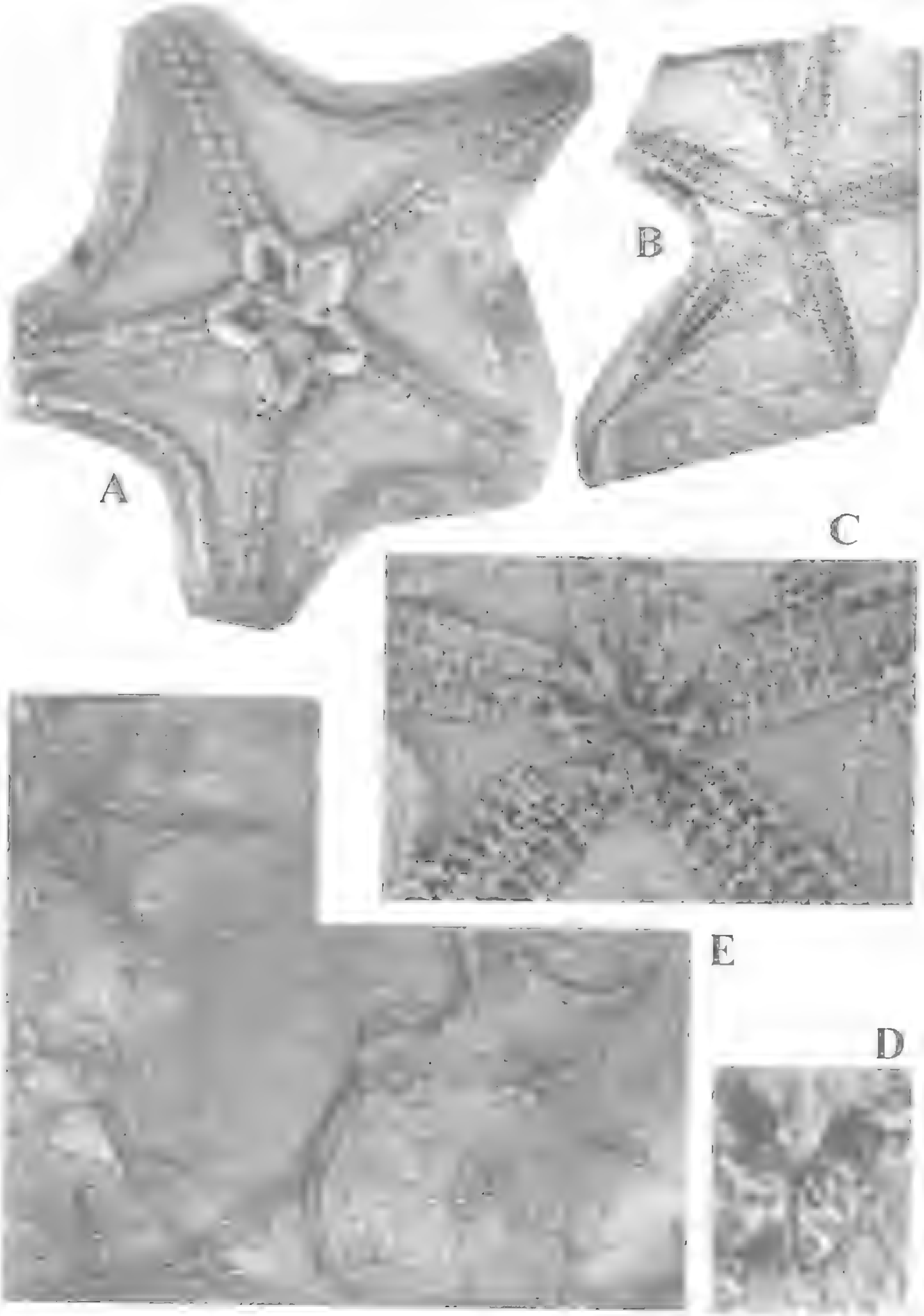



FIG. 40. *Encrinaster tischbeinianus* (Roemer, 1862). A, dorsal view of SAM K1018 ×2. B-D, ventral view of whole specimen, of disc area and of madreporite, respectively, SUG299, ×1.2, ×3.5 and ×15, respectively. E, slab with 3 individuals in ventral vie ×0.8 (figured by Spencer, 1950, figs 4, 5)

particularly Spencer accept that ambulacrals and adambulacrals could rotate in a transverse direction (ab.-ad.) and this is reflected in width of the ambulacral groove which varies from specimen to specimen. We suggest that such rotation is gretly restricted in the disc but not so restricted in the free arms. Therefore, we suggest that the specimens with wide adambulacrals in the proximal free part of the arm are ones where the adambulacrals have rotated laterally to expose their full width in dorsal view. Thus width of adambulacrals in direct dorsal or ventral view may often be influenced by the attitude in which a specimen is buried (i.e., whether adambulacrals are curled ventrally concealing much of the ambulacrals or flattened out on the sediment and often dislocated from the ambulacrals. In some instances, particularly where preservation is in fine mudstone, the degree of convexity of the arm is greater where the adambulacrals appear narrow and least where the adambulacrals appear widest; this suggests to us that rotation of the plates in the arm is a highly significant factor in determining the dorsal appearance of adambulacrals. Given the considerable width of the adambulacrals, small differences in attitude may make significant differences to perceived width. This feature must be considered unacceptable as a generic discriminator at least in the degree of widening. In the same key, Spencer (1930) distinguished a 3rd closely related genus, *Mastigactis* by its adambulacrals being of uniform width throughout the arm. Whether this uniformity is the result of the entire arm having been buried without any lateral rotation of the adambulacrals is not easy to determine without reference to the specimens and should remain an open question.

Recognising that a key seeks to limit the number of features by which to make easy recognition of taxa a search of discussion of the 2 genera following the key reveals very few comparative statements. Spencer (1930: 418) stated *Encrinaster* may be distinguished by comparatively long thin arms containing many segments and that marginal disc plates of *Encrinaster* bear long spines. The number of segments in each arm determines the length of the arm and the number increases with growth so this is a very growth related difference; measurements of all illustrated specimens of the 2 genera fail to show any clear cut differentiation. These linked and growth related features do separate the forms that Spencer (1930) figured in the work in which he erected the second genus. Similarly the long spines on the marginal plates in *E. grayae* are not evident in the type species or in most other species of the genus. Thus the features quoted by Spencer (1930) are parochial in their discriminatory application and are not suitable generic features on a broader scale. Thus we synonymise *Encrinaster* and *Euzonosoma*.

### **Encrinaster tischbeinianus** (Roemer, 1863) (Figs 40-43)

*Aspidosoma tischbeinianum* Roemer, 1863: 144, pl. 23, fig. 1a, b (not pl. 25, fig. 11); Schöndorf, 1910: 23 and synonmy listed therin.
*Encrinaster tischbeinianus* (Roemer): Schuchert, 1914: 244.
*Euzonosoma tischbeinianum* (Roemer): Spencer, 1930: 404; Lehmann, 1957: 25, pl. 4, figs 1, 4-6.
*Hexura weitzi* Spencer, 1950a: 300, figs 4, 5 (not figs 1-3).

MATERIAL. South Africa. B4500-4502, B4505, B4506, B4510, B4511, B4548 from the Voorstehoek Formation at Hottentots Kloof. SAMK1018 from Riet River N of Ceres on Wupperthal road. S side of farm which is also called Groote Rivier in the neighbourhood, from Voorstehoek Formation. SAM11908 from Gamkapoort. SUG299 from De Doorns. Spencer's specimen (1950a, figs 4,5). B4555 from Boplaas Farm in the Waboomberg Formation. B4563 from Swaarmoed Pass, 2.1km from Great Swaarmoed Farm, near Ceres. RUGDNH2 from the Tra-Tra Formation.

DIAGNOSIS. Reaching large size (130mm arm length); with arms distally whip-like; disc with concave margins (of more than 11) large plates between arms; rest of disc of thin tiny tuberculate plates; 1st ambulacrals short and stubby; ambulacral groove wide across disc (apparently unable to close?); ambulacrals and adambulacrals as boot-shaped ossicles with toes pointing at each other; podial basins circular, similarly sized throughout arm; width of arm determined by width of ambulacrals or attitude of adambulacrals; madreporite ventral, adjacent to mouth frame, with strong ridge ornament.

DESCRIPTION. *Overall form.* Arms up to 130mm long (95mm max. in South African material), petaloid, widest at disc margin (up to 5mm), tapering strongly in distal part, distally whip-like. Disc pentastellate, with concave disc margins between arms, diameter 7-40mm, 0.5 or more of arm length, with margin of large irregularly polygonal plates sometimes extending a 2nd or 3rd row away from margin, remainder of surface a tuberculate apparently lightly mineralised integument, with larger tubercles close to mouth frame ventrally, especially in larger specimens.
*Arm plating.* Within the disc arms fixed into the plating, with adambulacrals and ambulacrals on

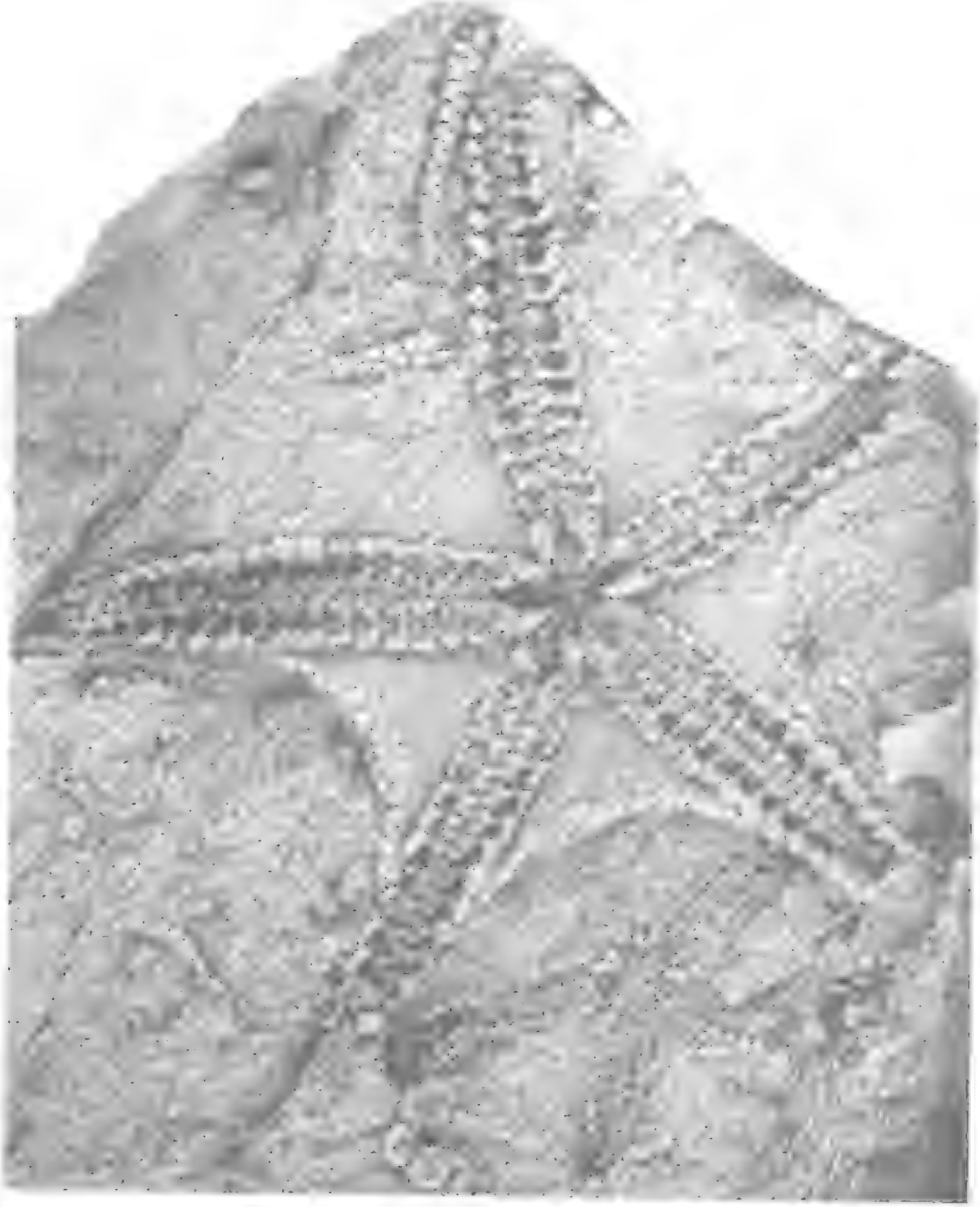


FIG. 41. *Encrinaster tischbeinianus* (Roemer, 1862). Ventral view of adult holotype with numerous fragmentary juveniles in both ventral and dorsal views. B4501 ×3.5

same level suggesting ambulacral groove may be wide open and unable to be closed. Towards disc margin adambulacrals extending ventrally beyond ambulacrals and laterally enclosing a wide, deep ambulacral groove. Within disc, ambulacrals wide, with boot-shaped ridges well

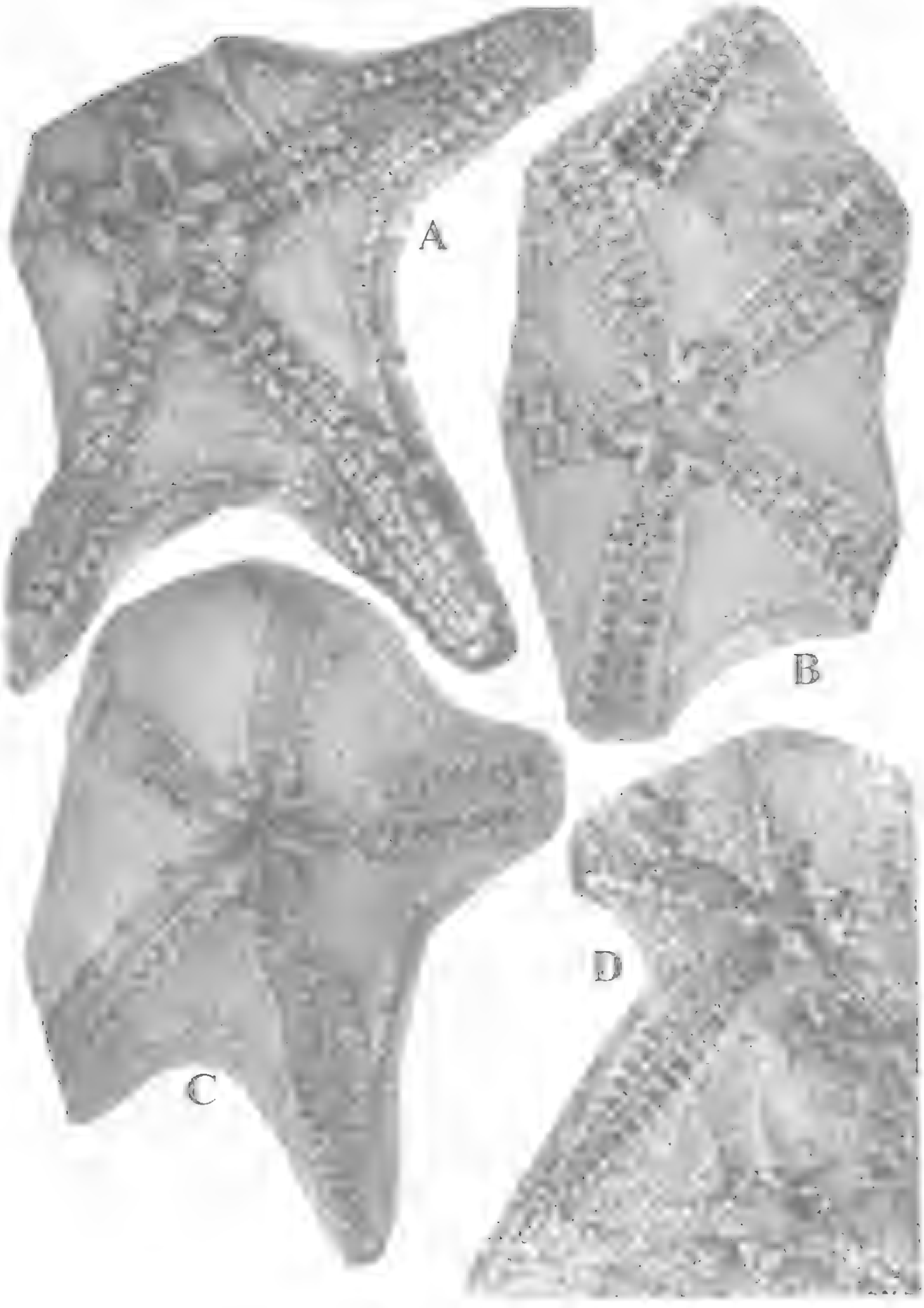
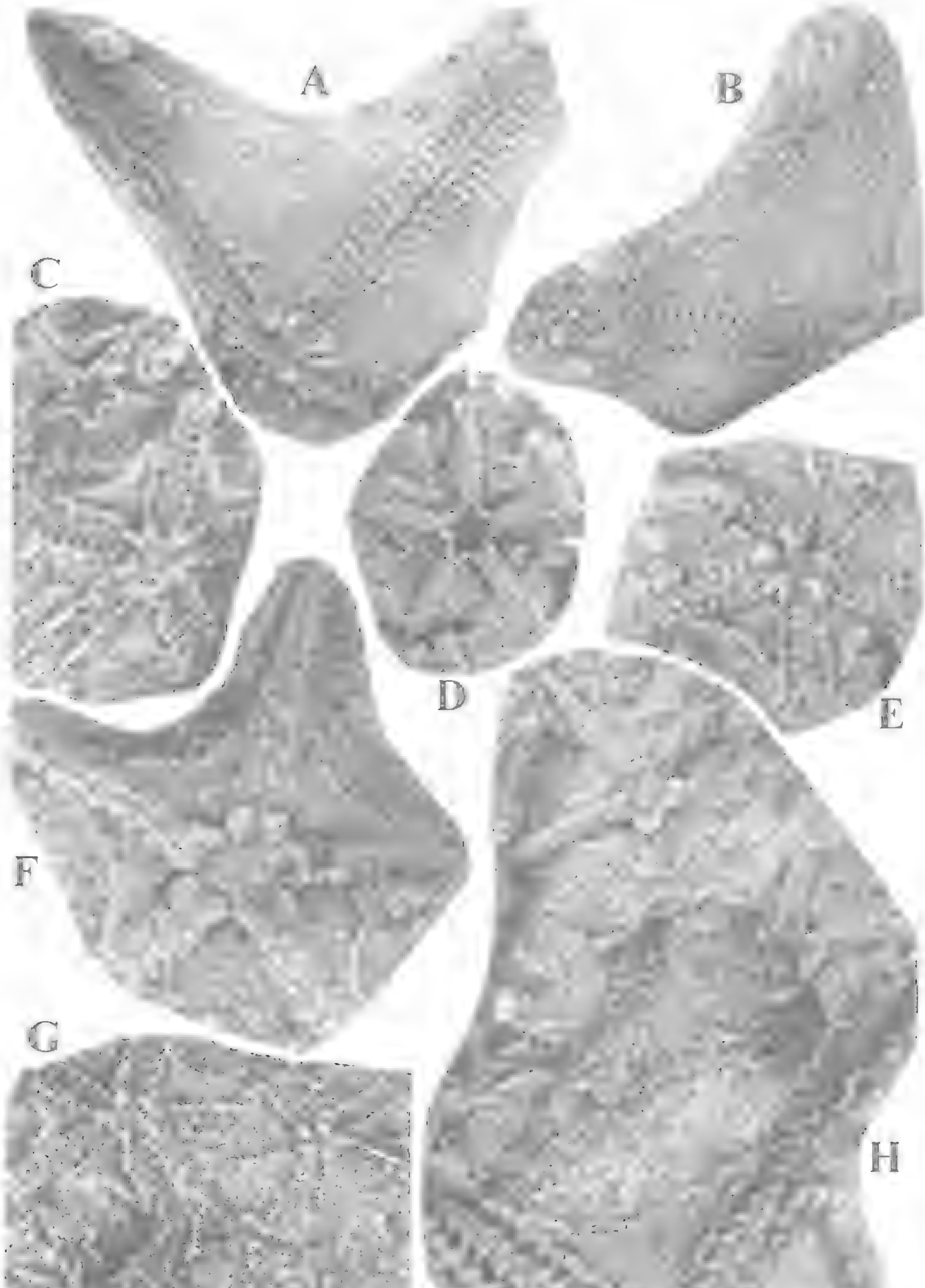



FIG. 42. *Encrinaster tischbeinianus* (Roemer, 1862). A, dorsal view of incomplete B4555 ×3. B, C, ventral views of B4500 and SAM11908, respectively ×2. D, incomplete ventral view B4567 ×4.



away from the arm axis; near the disc margin, boot-shaped ridges closer to axis but arm of same width; distally, boot-shaped ridges contiguous along arm axis; ambulacrals narrowing abruptly to produce the whip-like termination.

Ambulacrals offset across arm axis; in dorsal view subquadrate, with narrow (becoming wider in larger specimens) but deep elliptical clefts between successive plates formed by concave proximal and distal faces for muscle insertion; proximal and distal margins raised as low ridges, with posterior rim extending abradially, with dorsal rim of concavity raised as a transverse ridge proximally, becoming less distinct distally as the interambulacral cleft becomes smaller and dorsal surface becomes subcylindrical (i.e., flat radially but curved transversely). Laterally this subcylindrical surface changes at a sharp line into a gently convex adradial side to the podial basin. Podial basin with floor having circular gap in the plates between ambulacrals and adambulacrals.

In ventral view, sutural junction between the 2 columns of ambulacrals obtusely zigzag (c. 160°). Proximal arm with thin, low, uniform, radial ridge along ambulacrals on each side of and close to (<0.5mm) arm axis; these ridges running to the suture along arm axis at about the disc margin. Abradial to this line each ambulacral with concavity facing arm axis and inclined on the side of the leg of the boot-shaped ridge. Prominently raised boot-shaped ridge with a strong constriction above the ankle and a long toe with distinct arch of the sole. Narrowest point (above the ankle) at midlength of podial basin on abradial side; small concavity (mentioned above) on adradial side. Abradial side concave, descending rapidly into the podial basin. Distally in the whip-like portion of the arm ambulacrals much narrower, lacking podial basins.

*Adambulacrals.* Shape and orientation of plates varying along column, with concommitant change in the ambulacral groove; ambulacrals 1 and 2 without associated adambulacrals. Adambulacrals proximally in dorsal view subtriangular, flat, in the same plane as the interradial surface, with articulation against ambulacrals a point separated from distal point by curved margin to aperture in floor of podial basin. Distinct groove parallel to axis along dorsal surface close to abradial margin, continuing along 6 plates beyond the disc margin, petering out as dorsal view of adambulacrals becomes progressively narrower. Adambulacrals changing from horizontal to almost vertical approaching disc margin, developing en echelon rather than linear arrangement; on 1 arm of the holotype 3 adambulacrals with bases of small spines attached to distal face (no other spines known). Adambulacrals almost vertical and subquadrate in lateral view just beyond the disc, distally becoming thinner, closer to the radial axis and enclosing arm more completely.

In ventral view, adambulacrals within disc as prominent L-shaped ridge with toe of base abutting against toe of boot-shaped ridge on ambulacral, with longer sections aligned and forming abradial margin of arm. Transverse ridge formed by toes of adjacent ambulacral and adambulacral almost knife-edged, of uniform height across both plates, giving very quadrate appearance to arms. Along abradial margins the continuity from plate to plate gives a sharp ridge along the whole arm to the disc margin. Gently sloping platform on adradial side of the L-shaped ridge descending into podial basins, formed by adradial face of adambulacral with ventral face directed laterally in this section of the arm. Approaching the disc margin podial basins smaller and deeper and adambulacrals arranged en echelon in column continuing so distally as adambulacrals become smaller but enclose the ambulacral groove more.

*Mouthframe.* 1st and 2nd ambulacrals conspicuous; tori and denticles rarely evident (dorsal margin of 1 torus (Fig. 42A) and a set of 3 denticles attached to a torus (Fig.41) are evident). 1st ambulacral with proximal ends vertical, bluntly pointed; groove for nerve ring extremely well impressed distal to where 1st Amb becomes higher and wider; groove for water ring wider and shallower, remaining on the mouthframe plates across the radial and interradial sutures so that the groove is evident as a full ring, with 2 pores in the groove on each 2nd ambulacral near the radial line of each arm. At the interradial junction between 1st ambulacra the water ring groove descends into the junction, creating a subcircular basin. 2nd ambulacral expanded only slightly distally, barely overlying any of 3rd ambulacral.

FIG. 43. *Encrinaster tischbeinianus* (Roemer, 1862). A-B, large incomplete individual in ventral and dorsal views, respectively, RUGDNH2 ×1.2. C,D, juvenile in ventral view, B4500 ×2. E, juvenile in ventral view, B4548 ×3. F, juvenile in dorsal view B4502 ×7. G, group of juveniles, B4500 ×2. H, group of juveniles, with adult at bottom, B4502 ×3.

In ventral view, proximal faces of adjacent 1st ambulacrals forming high concave recess to accommodate tori. 1st ambulacral extending well ventrally at edge of the mouth, descending steeply distally; suture between 1st and 2nd ambulacrals about halfway down this slope at widest point. 2nd Amb with small shallow podial basin on distal adradial corner and beginning of sharp longitudinal ridge of adambulacrals on distal abradial corner. Distal face of 2nd ambulacral near arm axis with small concave facet opposing the same on 3rd ambulacral, both for insertion of longitudinal muscles.

*Madreporite*. Interradially on ventral surface, just to the right of and contiguous with 2nd ambulacral, oval, outwardly convex, with irregular straight and curved grooves peripherally.

*Disc*. Dorsal surface a tessellated pavement of thin subquadrate to irregular plates each bearing a rounded tubercle, with margin of superior and inferior series of larger, thicker, differentiated plates without tubercles and with well defined sutural interplate boundaries. A few such plates are rarely seen in the second row from the margin.

REMARKS. Dorsally, available specimens show the plating of the mouthframe and arms without any suggestion of integument covering them; in life there must have been some sort of integument over the central mouth area and this probably extended out over the arms as well. It is probably of some unmineralised tissue that does not fossilise. How such an unmineralised integument related to the interradii is not clear; the obvious arrangement would see a 'skin' enclose the whole disc but then the reason for tubercles on plates becomes unclear if they are internal. If the integument covered only the mouth frame and arms the arrangement for its connection to the body between adambulacrals and interradial plates and its method of growth are obscure. Adambulacrals within disc have sutural junctions with the interradii on dorsal and ventral surfaces so the height of the body could not have been more than 1-2mm at this point as that is the height of the abradial wall of adambulacrals; this would leave a very flat body cavity within the disc and adds support to the possibility of an outer integument covering the entire body except for the ambulacral grooves and mouth.

This South African material conforms closely to the German *E. tischbeinianus* from the Lower Devonian Hunsrückschiefer in all features including relative disc size and shape, number of marginal disc plates, arm shape, relatively widely separated ambulacral column in each arm, and size and shape of the mouth frame. Considerably larger specimens are known from Germany but this disparity may be accounted for by the amount of collecting and by the German slates being a better matrix for yielding large whole specimens; in the coarser South African matrix the chances of obtaining large specimens is reduced. The finely tuberculate ornament on the disc is not evident on the German material but the slatey cleavage would be expected to obliterate such fine ornament. We consider all these discrepencies due to differences in preservation or intraspecific.

A number of very small specimens among the South African material give some information on growth of the species. In general the small specimens are virtually identical to the larger ones except that the mouth frame is not so robust, particularly in dorsal view; the arms appear to be of uniform width and the abradial aligned parts of the adambulacrals remain narrow and knife-edged throughout instead of thickening up and becoming en echelon arranged as in the larger specimens.

### **Marginura** Haude, 1999

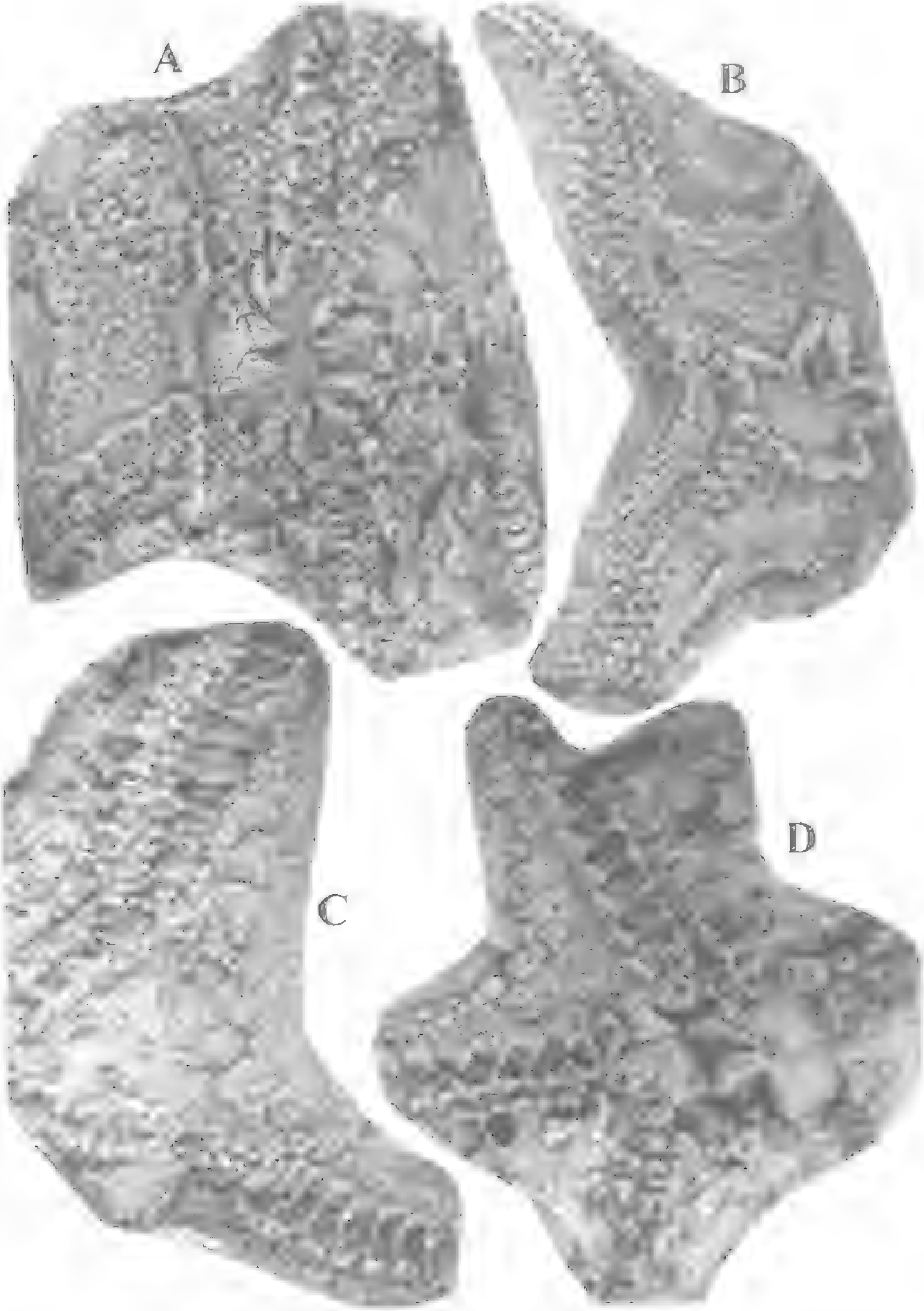
not *Marginaster* Perrier, 1881;
*Marginaster* Haude, 1995: 63.
*Marginura* Haude, 1999: 1.

TYPE SPECIES. *Encrinaster yachalensis* Ruedemann, 1916 from the Lower Devonian of western Argentina.

DIAGNOSIS (from Haude, 1995). Encrinasterinae with mosaic plated dorsal surface and interradii, concave margins to disc, concave outer margin of podial basin which has a round upper lamella.

REMARKS. This genus is only known from South America (Haude, 1995) and now South Africa.

FIG. 44. *Marginura hilleri* sp. nov. A, ventral view of disc including slightly disarticulated oral area B4566 ×3. B, dorsal view of incomplete specimen RO P84B ×3. C, ventral view of parts of 2 arms and an interradius with only marginal plating of latter remaining RO P84C ×5. D, ventral view of 2 arms, an interradius and the oral area with plates adjacent to mouth mainly disociated and possible madreporite at lower right RO E11 ×3.


A
B
C
D

**Marginura hilleri** sp. nov.
(Figs 44, 45)

ETYMOLOGY. For Dr Norton Hiller who contributed material for this study.

MATERIAL. HOLOTYPE: B4566 from Swaarmoed Pass, Ceres, 1.3 miles from Great Swaarmoed Farm. RO E11 from Damascus, Prince Albert at 33° 17'15"S; 21° 55'45"E. ROP84 from Swaarmoed Pass, Ceres at 33°21'30"S; 19°30'30"E.

DIAGNOSIS. Disc surface a mosaic of polygonal plates; disc plates larger and subquadrate near the margin, much smaller, less regular and bearing strong circular tubercles proximally. Adambulacrals with club-shaped abradial expansion, with L-shaped ridge running along proximal and then abradial margins. Ambulacral 2 extending dorsally over 3rd and 4th and with pointed distal extremity (not truncated). Abradial spatulate spines on arms apparently continuing along interradial disc margin.

DESCRIPTION. *Overall form*. Arms up to 40mm long, tapering distally, distally whip-like. Disc pentastellate, with concave disc margins between arms, with margin of large irregularly polygonal plates bearing marginal spines (2 per marginal), remainder of surface of small irregular tuberculate plates.

*Arm plating*. Within the disc arms fixed into the ventral plating. Distally adambulacrals extending further ventrally to enclose a narrowing but deeper ambulacral groove. [Within disc ambulacrals wide, with boot-shaped ridges well away from the arm axis; near the disc margin boot-shaped ridges closer to axis but arm of same width; distally boot-shaped ridges contiguous along arm axis; ambulacrals narrowing dramatically to produce the whip-like termination.]

Ambulacrals offset across arm axis, with straight intercolumn suture along arm axis, proximally much wider than long in dorsal view but in 2 distinct sections: 1, a subquadrate raised adradial section with 1-2 tubercles on a fine granular background ornament and 2, an abradial section down a distinct abradial slope (abradial section becoming narrower distally along arm and disappearing at beginning of whip-like section), with wide deep elliptical clefts between successive plates formed by concave proximal and distal faces for muscle insertion; proximally dorsal proximal and distal margins with fine low ridges.

In ventral view arm axis with straight sutural junction and distinct ambulacral channel between the 2 columns of ambulacrals; each ambulacral concave towards arm axis (i.e. back of leg of boot shape). Prominently raised boot-shaped ridge with short leg, strong constriction above the ankle and a long toe with distinct arch of the sole; with narrowest point (above the ankle) at midlength of podial basin, with concave abradial side descending rapidly into the podial basin. Ambulacrals much narrower distally in the whip-like portion of the arm, apparently lacking podial basins.

*Adambulacrals*. Shape and orientation of plates varying distally along column, shaped like the head of a large golf club (a 'wood') with transverse projection (the shaft of the golf club) abutting the toe of the ambulacral 'boot'; ambulacrals 1 and 2 without associated adambulacrals. Adambulacrals subquadrate in dorsal view, with articulation against ambulacrals at 2 points (anterior and posterior), with concave adradial margin in between combining with concave abradial margin of ambulacrals to define perforation through bottom of podial basin. Adambulacrals vertical throughout, forming lateral wall of arm.

In oral view, adambulacrals very thickened abradially, with continuity from plate to plate of expanded abradial parts producing sharp ridge along the whole arm being base of lateral wall, with gently sloping platform on adradial side descending into podial basins, with short wide spatulate lateral spines.

*Mouthframe*. 1st and 2nd ambulacrals fused into large unit as typically forms mouth frame throughout family but suture between them not evident on available material, dorsally overriding 3rd and 4th ambulacrals; tori and denticles not evident but a few acicular plates in oral region of one specimen (Fig. 44B) may be disaggregated denticles, with small narrow proximal ends; groove for nerve ring shallow and crossing paired 1st ambulacrals just proximal to groove for water vascular ring; groove for water ring wide, well-impressed, remaining on the mouthframe plates across the radial and interradial sutures (so that the groove is evident as a full ring), with 2 pores in the groove on each 2nd ambulacral near the radial line of each arm.

In ventral view, proximal faces of adjacent 1st ambulacrals forming relatively small concave recess to accommodate tori. 2nd Amb with small deep podial basin on distal adradial corner. Distal face of 2nd ambulacral near arm axis with small concave facet opposing the same on 3rd ambulacral, both for insertion of longitudinal muscles.

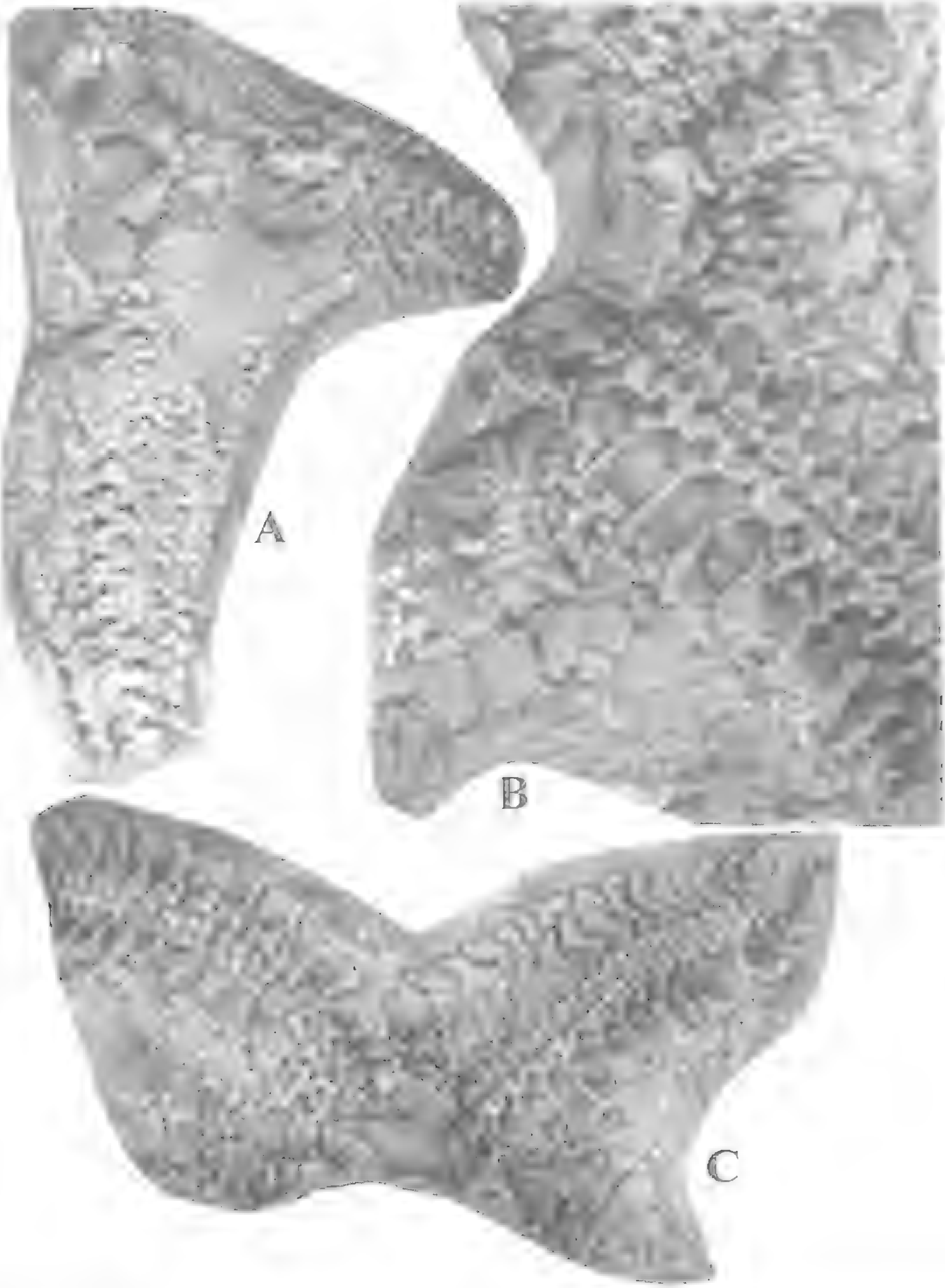



FIG. 45. *Marginura hilleri* sp. nov. RO P84a & b, incomplete holotype, 2 incomplete arms, an interradius and some oral plates. A, dorsal view ×5. B, enlargement of lower right of C showing madreporite (left) and short spiny interradial plates disarticulated and lying on their side ×7. C, ventral view ×5.

*Madreporite*. Interradially on ventral surface, suboval, with ornament of vermiform groove defined by sharp ridges.

REMARKS. This species is very close to the type and only congener, *M. yachalensis* but may be distinguished by its marginal spines, the pointed rather than truncated distal dorsal tips of the second ambulacrals, the course of the sharp ridge on the ventral side of the adambulacrals and the size of the tubercles or small spines on the ventral interradial disc plates, particularly proximally. The new species does not contradict any of the structural interpretation of Haude (1995).

Family PROTASTERIDAE Miller, 1889

**Eugasterella** Schuchert, 1914

TYPE SPECIES. *Eugasterella logani* (Hall, 1858) from the Middle Devonian Hamilton Group of New York.

DIAGNOSIS. Arms 5, long, slender, tapering distally, without dorsal arm plates or dorsal spines. Disc circular, inflated; dorsal surface of polygonal plates covered by finely granular integument. Madreporite ventral. Mouth frame large; 1st ambulacral long, narrow; 2nd ambulacral large, stout, with well-developed grooves, apophyses and pores dorsally for directing water vascular and nervous systems. Ambulacrals boot-shaped in ventral view; ambulacral groove slightly sinuous; dorsal surface with wide deep excavations for dorsal longitudinal muscles; podial basins large and well-defined. Adambulacrals roughly ear-shaped, narrow, wrapped around sides of ambulacrals, with large nodes for attachment to toe of boot on ambulacrals, with vertical spines.

REMARKS. This diagnosis follows that of Harper (1985) with emendation as inferred by Hotchkiss (1993) who diagnosed *Strataster*, emphasising features of dorsal arm structure.

**Eugasterella africana** sp. nov.
(Figs 46-48)

*Hexura weitzi* Spencer, 1950a: fig. 3 [not figs 1,2,4-6].

ETYMOLOGY. From Africa.

MATERIAL. HOLOTYPE: B4561a (a,b, dorsal and ventral external moulds). PARATYPES: B4561b and c all from Klipfontein near Swaarmoed Pass, Ceres, B4569 from Hex Rivier Pass on Montagu Road 14km from N9 turnoff and RO123 from Matroosberg, Worcester(Hex River Pass) (33°30'S, 19° 48'E); all from the Voorstehoek formation. SAMK1014, 1015 from Verstehoek Formation at Riet Rivier (i.e. Gydo Formation, N of Ceres Division on Wupperthal Road; S side of farm which is also called Groot Rivier in the neighbourhood.

DIAGNOSIS. Arms slender, tapering gently throughout. Disc subrounded to subpentangular, inflated dorsally; dorsal surface of thin plates covered by a finely tuberculate integument, without spines. Short spines in a central marginal triangle on ventral interradii. Ambulacrals boot-shaped, with leg and foot of about same length. Adambulacrals with row of spatulate spines along ventral edge and 1-2 vertical spines. Madreporite circular with marginal aperture around half circumference.

DESCRIPTION. *Overall form*. 5-armed, disc radius 5-8mm, arm length up to 35mm. Arms slender, 2-3mm wide at disc margin, tapering distally throughout (no arm tip available). Disc circular to subpentagonal, gently inflated dorsally, with dorsal surface of small thin irregularly shaped plates covered by finely granular integument, without any spines on dorsal surface; ventral interradii triangular, with same finely granular integument as dorsal surface covering a lattice-like arrangement of plates increasing in aperture sizes towards margin of disc, with short stout spines in triangular zone involving entire disc margin and a third corner interradially about 1/3 disc radius away from margin.

*Arm plating*. Dorsal surface of arms circular in section, with many small thin irregular plates possibly elongate across arm axis and irregularly with small nodes. Ambulacrals offset along arm axis; in dorsal view subtrapezoidal, with wide deep excavations proximally and distally for longitudinal muscles, with prominent (decreasing in prominence distally) transverse ridges proximally and distally above deep cleft for muscle attachment, slightly sinuous axial line formed by concave adradial margin on each ambulacral into which a proximal and distal tip of successive ambulacrals from the opposite column project, the sinuosity decreasing distally; ventrally boot-shaped, with leg and foot of about equal length; ambulacral groove shallow, slightly sinuous as in dorsal aspect; podial basin round, deep, almost entirely on 1 ambulacral with corresponding adambulacral forming outer side to basin. Adambulacral abradial to and corresponding 1 to 1 to ambulacrals, planar, roughly ear-shaped, oriented vertically to form the lateral walls of the arm; in dorsal view only slightly abradially convex dorsal edge around short abradial edge of ambulacrals; in ventral


FIG. 46. *Eugasterella africana* sp. nov. A-B, ventral and dorsal views, respectively, of holotype B4561a & b ×4. C-D, dorsal and ventral views, repectively, of specimen with dorsal plating removed thus exposing proximal ambulacrals, tori and oral denticles (not evident with dorsal surface in place as in B) RO123a & b ×4.

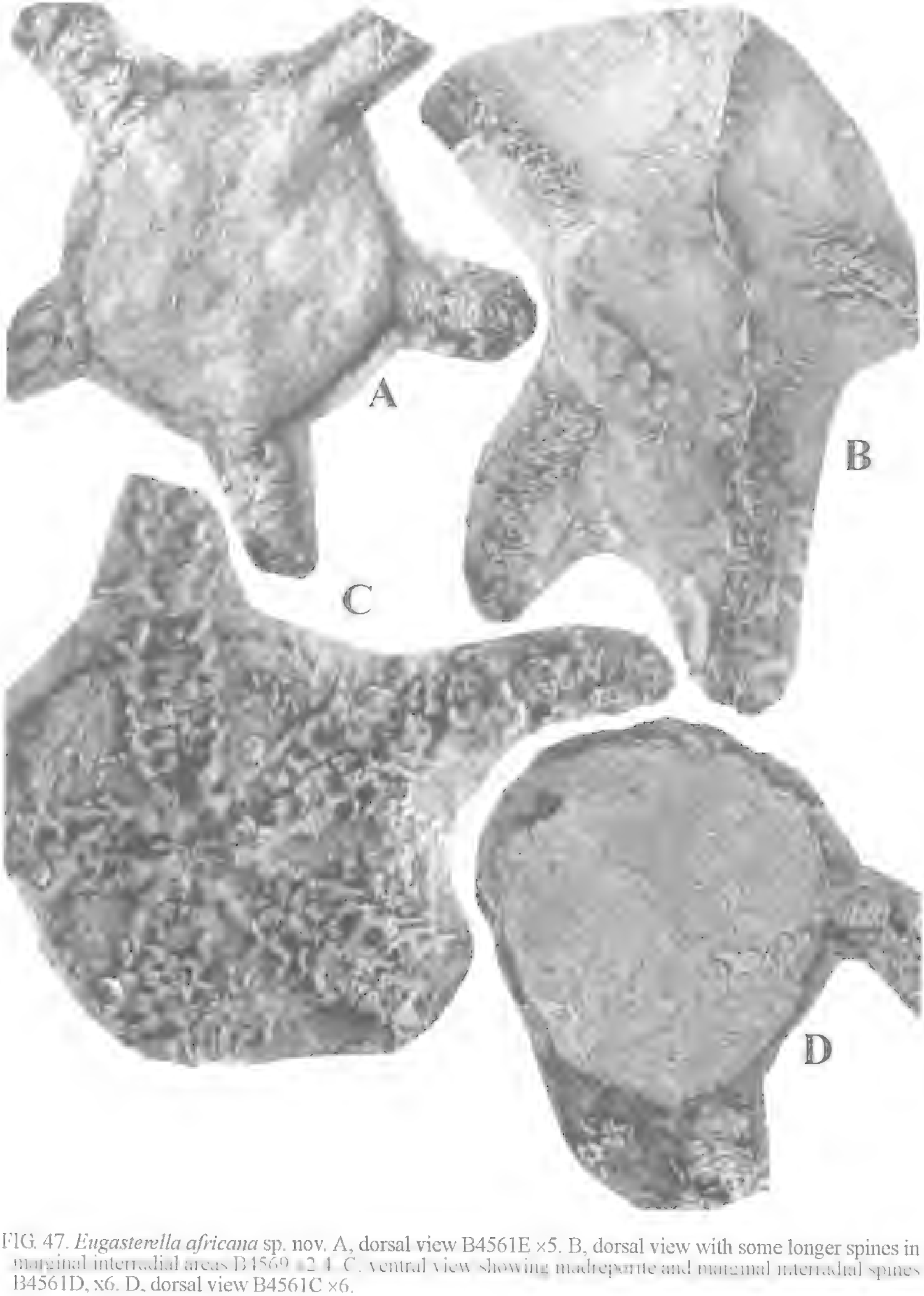



FIG. 47. *Eugasterella africana* sp. nov. A, dorsal view B4561E ×5. B, dorsal view with some longer spines in marginal interradial areas B4569 ×2.4. C, ventral view showing madreporite and marginal interradial spines B4561D, x6. D, dorsal view B4561C ×6.

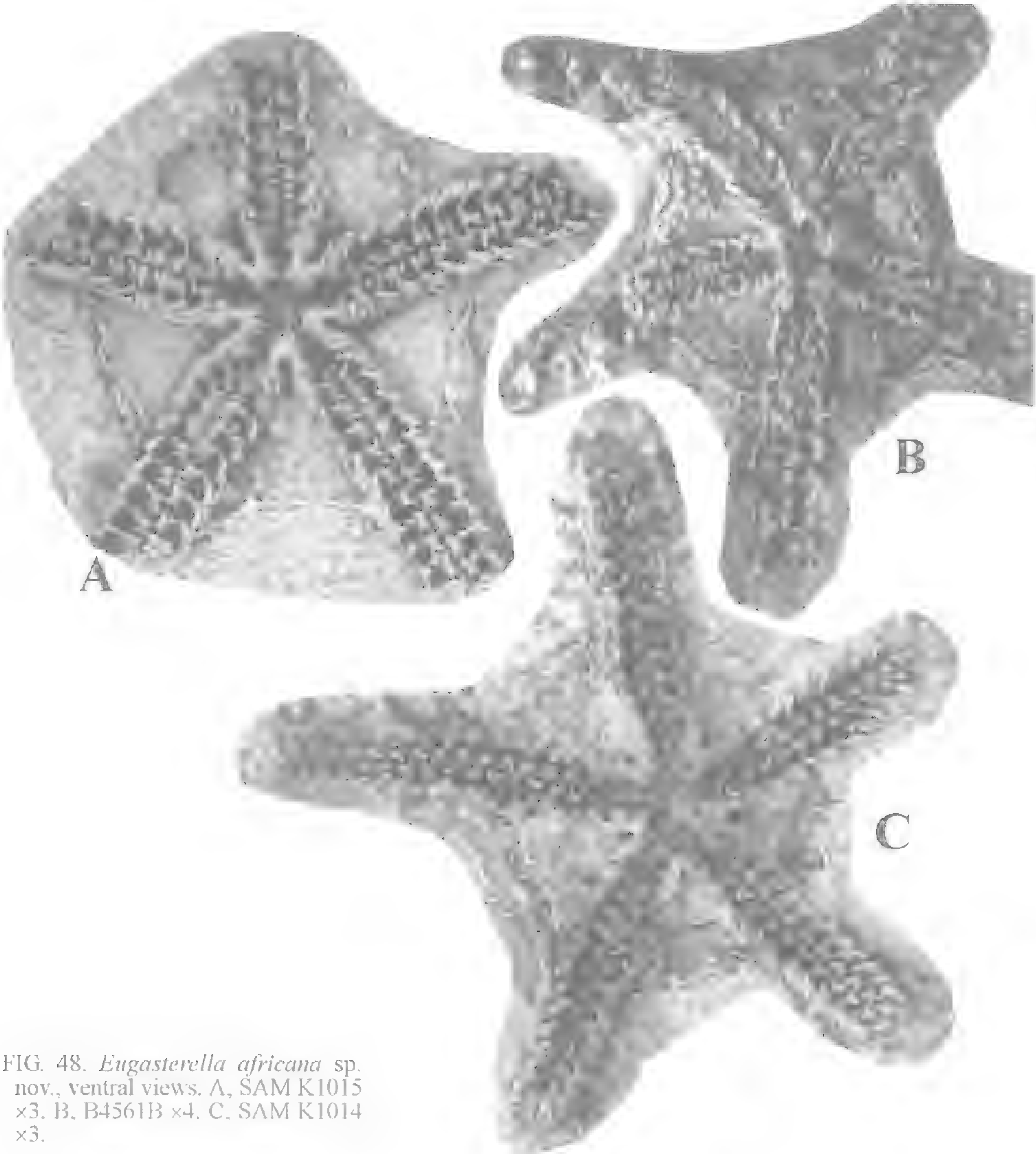



FIG. 48. *Eugasterella africana* sp. nov., ventral views. A, SAM K1015 ×3. B, B4561B ×4. C, SAM K1014 ×3.

view L-shaped, formed by strong lateral projection abutting toe of ambulacrals and narrow ventral edge in proximal-distal line, with line of 5 pits along narrow ventral edge each bearing short spatulate ventrally directed spine, with strong pointed spine directed distally arising from narrow platform formed by interruption to ventral edge towards distal end.

*Madreporite*. Ventral, to left in CD interradius, circular, convex, with broadly U-shaped slit-like opening close to and around 1/2 the circumference facing the D ray.

*Mouth frame*. In dorsal view occupying about 1/2 disc area; 1st ambulacrals in contiguous pairs interradially, elongate radially, straight, with transverse groove for nerve ring, pointed distal tip, with junction to 2nd ambulacral at 45° on outer distal bevelled face. Torus biconvex, fitting into concave proximal end of each pair of 1st ambulacrals, with horizontal row of 5 flat blunt

spines projecting into mouth (central 3 wider than others); 2nd ambulacral large, forming strong V distally along arm, extending over next 2 or 3 ambulacrals, with groove for water vascular system on proximal side, extending along proximal 1/2 across distal ends of 1st ambulacrals, with 2 pits in groove on each plate (leading to podial basins of 2nd and 3rd ambulacrals. In ventral view 1st ambulacrals paired, forming narrow Vs, not contiguous as in dorsal view, straight, with concave proximal face, abutting 2nd ambulacrals on abaxial side of podial basin; 2nd ambulacrals with well-developed podial basin beginning column of basins of each arm; reduced adambulacral with 5 spatulate ventral spines not visible in dorsal view where covered by expanded 2nd ambulacral.

REMARKS. This species differs from the type, *E. logani* (Hall, 1858), from the Middle Devonian of New York in having marginal interradial spines on the disc, ambulacrals shorter and with deeper longer dorsal clefts between successive ambulacrals in each column and circular madreporite with slit-like aperture around most of its margin; it resembles more the only other assigned species, *E. devonicus* (Kesling, 1972) from the Middle Devonian of Ohio, in structure of the disc and in spinosity of adambulacrals although it appears to have a maximum of 2 vertical spines on each adambulacral as opposed to 4 in the North American species and may be further distinguished by the structure of the disc dorsally, which in *E. devonicus* was described by Kesling as having no discernible plates, thickly studded with small grains probably marking the position of papillae and bristly with short erect little spines.

Harper (1985, fig. 5) described and figured the dorsal surface of the disc of *E. logani* as composed of overlapping polygonal plates bearing raised biaxial ridges. The South African species suggests that these ridged plates are part of the ventral interradial plating (Figs 46C, D) which are evident in both dorsal and ventral moulds of specimens where the dorsal surface of the disc has been removed. We would interpret Harper's figure (1985, fig. 2C) as representing a specimen in which the dorsal surface of the disc was well-preserved only in the interradial triangle on the right of the specimen as viewed; some dorsal surface is evident in the other interradial areas except that at the upper left where the ventral or inner surface of the ventral plating is evident.

**Stratasater** Kesling & Le Vasseur, 1971

TYPE SPECIES. *Stratasater ohioensis* Kesling & Le Vasseur, 1971 from the Lower Carboniferous of Ohio; by original designation.

DIAGNOSIS. See Hotchkiss (1993:64).

**Stratasater ohioensis**
Kesling & Le Vasseur, 1971
(Figs 49-53)

MATERIAL. South African material - B4509, B4512, B4513, B0195 -0197, B0276 and PRVT82 all from Boplaas Farm, N of Ceres in the Waboomberg Formation.

REMARKS. Some of these external moulds were coated with a thin layer of varnish after collection; this made them less absorbent and thus the latex casting has not been as successful as with other unvarnished material. The dorsal crest of each arm usually has a row of small air bubbles where the latex did not penetrate into the moulds of the carinal spines, but these spines are cast in a few places (Fig. 50C, 51B). The papillate dorsal disc integument is well preserved in several places draped over the strong mouth frame exactly as with Kesling and Le Vasseur's (1971) material; this indicates that the disc was distended with fluid or other soft tissue during life but had no solid material in it and no detritus in the gut. This is in contrast to *Eugasterella africana* where the disc has remained inflated indicating some solid disc filling such as sediment detritus or some structural integrity possibly conferred by the dorsal plating beneath the papillate surface.

This material agrees with the species described by Kesling & LeVasseur (1971) in every respect and as those authors gave an extremely detailed description there is nothing further to add. In particular, the upper arm plates and row of carinal spines, considered by Hotchkiss (1993), to be generic features occur in the South African material. The dorsal clefts between ambulacrals appear sharper in some of the North American specimens but in the South African material the small dorsal arm plates are preserved in most places and the varnish applied to the external moulds has in most cases diminished the height of the ridges adjacent to the dorsal clefts.

The South African occurrence extends the range to become Early Devonian to Early Carboniferous (Tournaisian) and the geographic extent to include Laurentia and Gondwanaland encompassing the Appalachian and Malvinokaffric

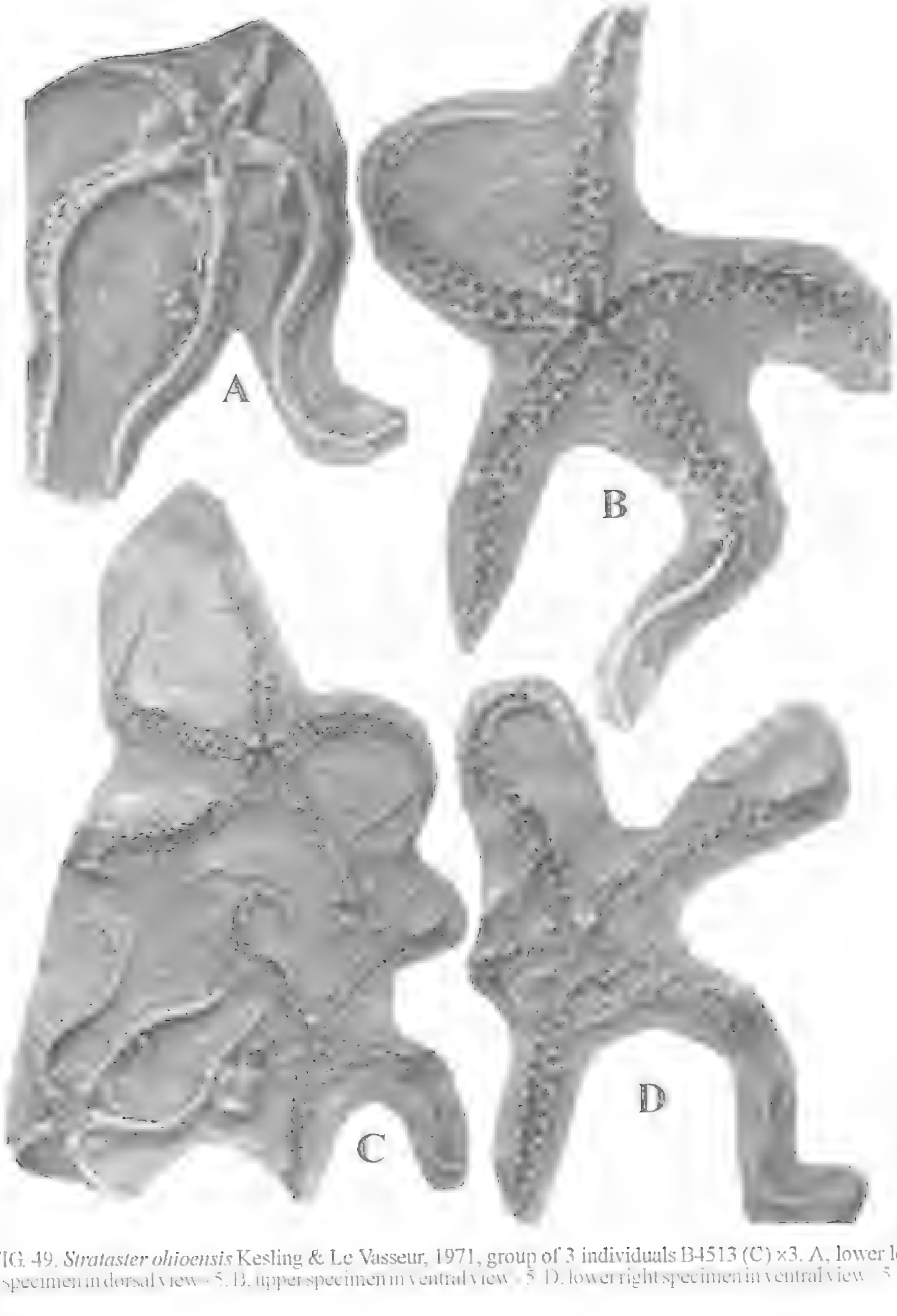



FIG. 49. *Strataster ohioensis* Kesling & Le Vasseur, 1971, group of 3 individuals B4513 (C) ×3. A, lower left specimen in dorsal view ×5. B, upper specimen in ventral view ×5. D, lower right specimen in ventral view ×5.

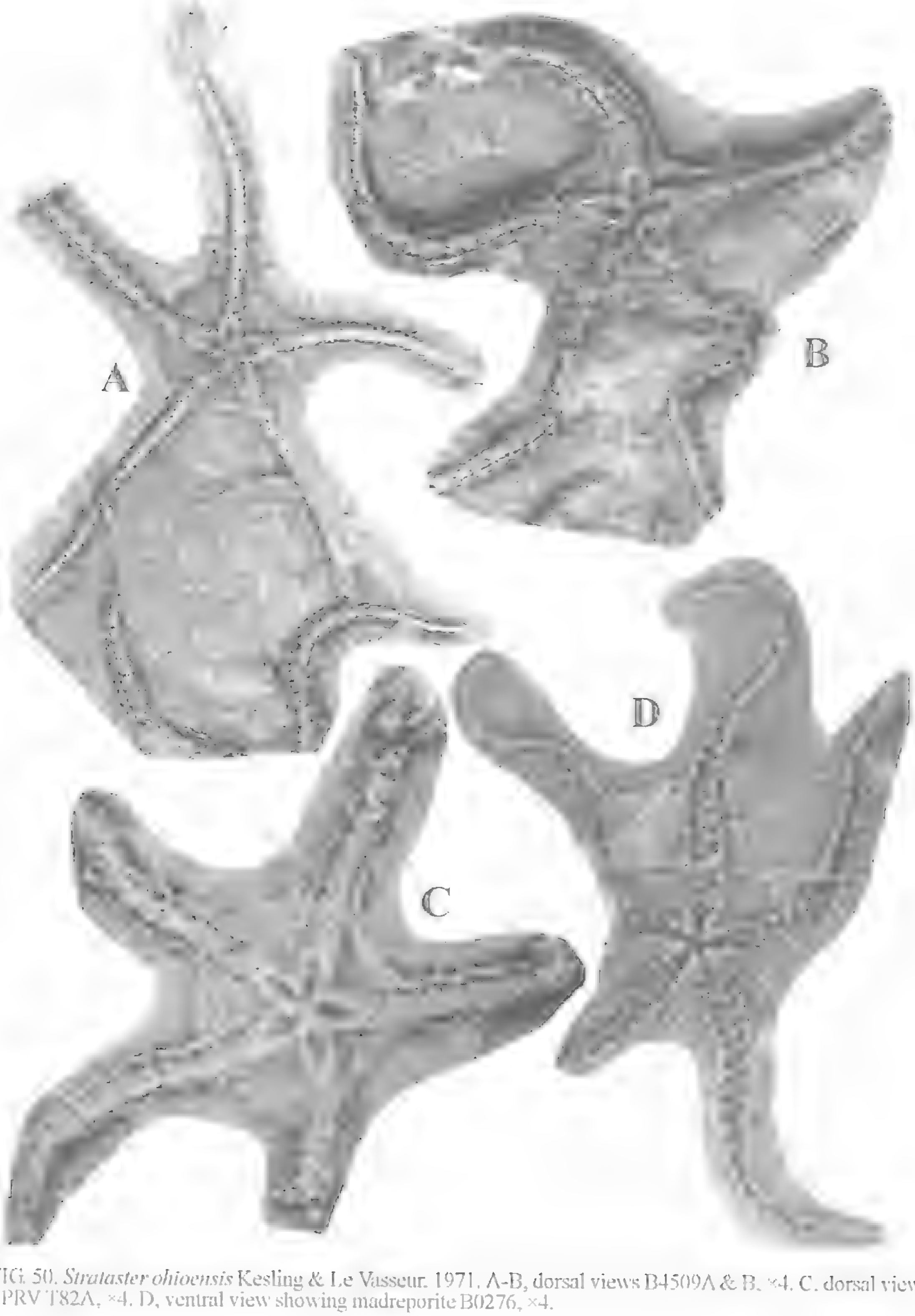



FIG. 50. *Strataster ohioensis* Kesling & Le Vasseur. 1971. A-B, dorsal views B4509A & B, ×4. C, dorsal view PRV T82A, ×4. D, ventral view showing madreporite B0276, ×4.

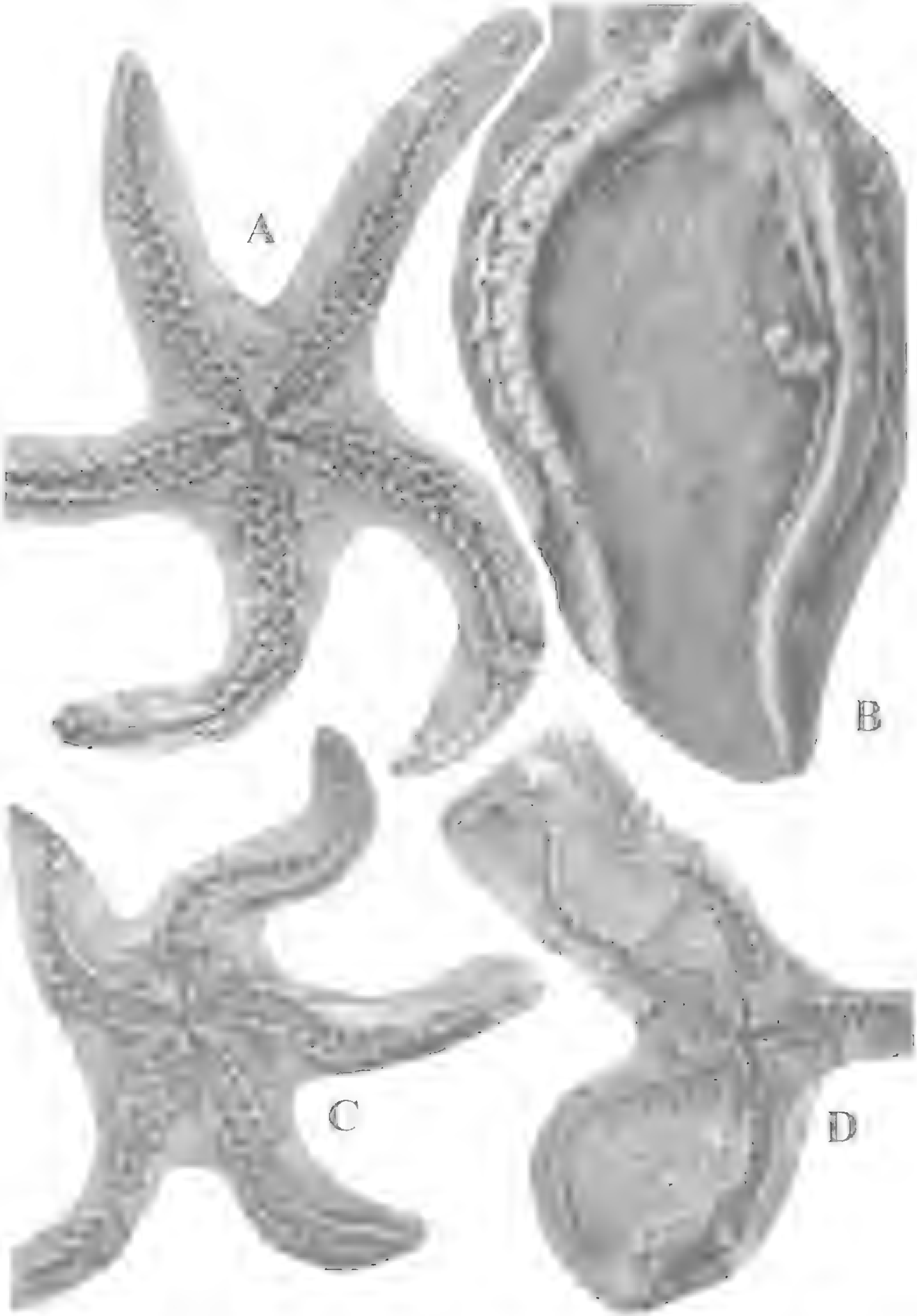



FIG. 51. *Strataster ohioensis* Kesling & Le Vasseur, 1971. A, ventral view PRV T82B, ×6. B, enlargement of 2 arms from Fig. 37A to show the median row of dorsal spines on each B4513, ×10. C, ventral view B0196, ×4. D, ventral view B0276, ×4.

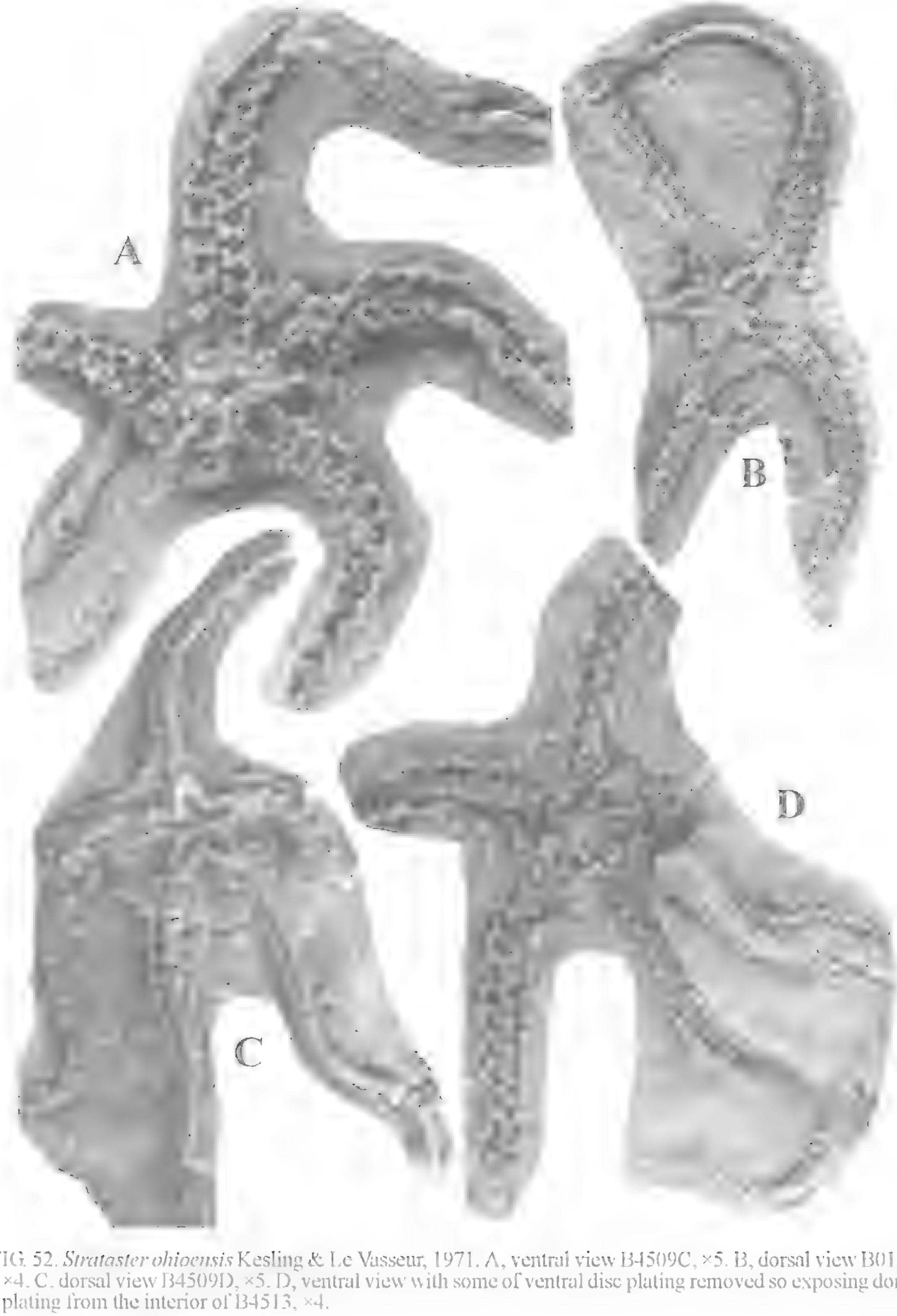



FIG. 52. *Strataster ohioensis* Kesling & Le Vasseur, 1971. A, ventral view B4509C, ×5. B, dorsal view B0197, ×4. C, dorsal view B4509D, ×5. D, ventral view with some of ventral disc plating removed so exposing dorsal plating from the interior of B4513, ×4.

FIG. 53. *Strataster ohioensis* Kesling & Le Vasseur, 1971, ventral view of large individual B4512 ×3.

Provinces of brachiopod palaeobiogeography (Boucot et al., 1969).

Some of the material referred to by Hotchkiss (1995) in his Appendix 1 at numbers 108-112 is included in this species.

**Strataster stuckenbergi** (Rilett, 1971) (Figs 54-56)

*Taeniaster stuckenbergi* Rilett, 1971: 32, figs 3-4.

MATERIAL. HOLOTYPE: NM Type 1550 on NM831 from near Ceres. OTHER MATERIAL: B4504 from the Waboomberg Formation at Theronsberg Pass, B4533, B4536 from the Voorstehoek Formation at Matroosberg.

DIAGNOSIS. Row of carinal spines on arms not extending onto disc or to arm tips. Disc integument dorsally and ventrally (interradii) with irregularly spaced spines on papillate surface. Ambulacrals with short leg and longer foot to boot in ventral view. Adambulacrals with 6 or 7 curved, spatulate, ventral (or oral) spines, with 2 or 3 strong, straight, circular-sectioned lateral (vertical) spines. Madreporite large, circular, with slit-like aperture adjacent and parallel to margin for about 3/4 circumference.

DESCRIPTION. *Size and shape.* Average disc diameter among available specimens 15-20mm. Disc apparently circular; a few specimens suggest the disc may be extended slightly down each arm to give a substellate shape but this is probably due to postmortem movement. All available arms are preserved in curved position but are estimated to be 40-50mm long; arms widest at edge of disc (up to 4mm), tapering strongly distally to be <1mm wide over distal 10mm. The disc must have been flexible to some extent because angles between arms are not equal in any individual; while some of this may be due to postmortem forces it does indicate some ability for the arms to move towards and away from each other at least at the disc margin.

*Ambulacrals.* Alternating in 2 rows either side of a straight midline. Individual plates subrectangular, wider than long proximally, becoming longer than wide distally. Boot-shaped ridge prominent in ventral view, with a stout leg, projecting tips both back and forward up the leg, a distinct arch to the foot and a long toe abutting against the adambulacral. Podial basin deep, entirely on ambulacrals (with adambulacrals forming lateral wall of basin only). Distally (in whip-like section) no ambulacral groove, adambulacrals abut each other along the ventral midline. Dorsally 2 transverse ridges on each ambulacral; proximally these are close together near the midlength of the plate and converge slightly abaxially; between ambulacrals these high ridges are separated by wide deep V-shaped clefts for insertion of dorsal longitudinal muscles. Distally along the arm

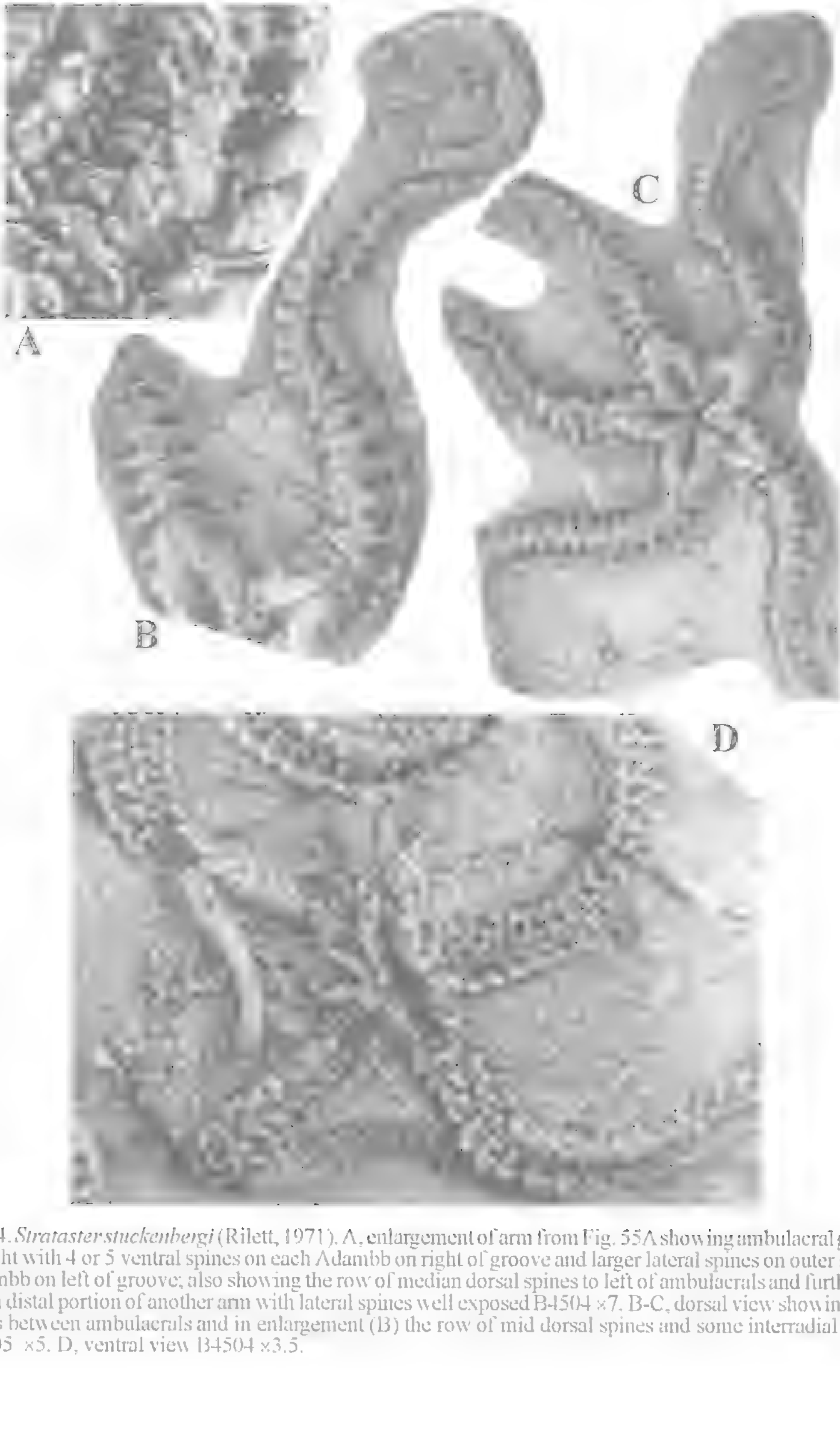


FIG. 54. *Strataster stuckenbergi* (Rilett, 1971). A, enlargement of arm from Fig. 55A showing ambulacral groove to right with 4 or 5 ventral spines on each Adambb on right of groove and larger lateral spines on outer side of Adambb on left of groove; also showing the row of median dorsal spines to left of ambulacrals and further left still a distal portion of another arm with lateral spines well exposed B4504 ×7. B-C, dorsal view showing deep clefts between ambulacrals and in enlargement (B) the row of mid dorsal spines and some interradial spines B4505 ×5. D, ventral view B4504 ×3.5.

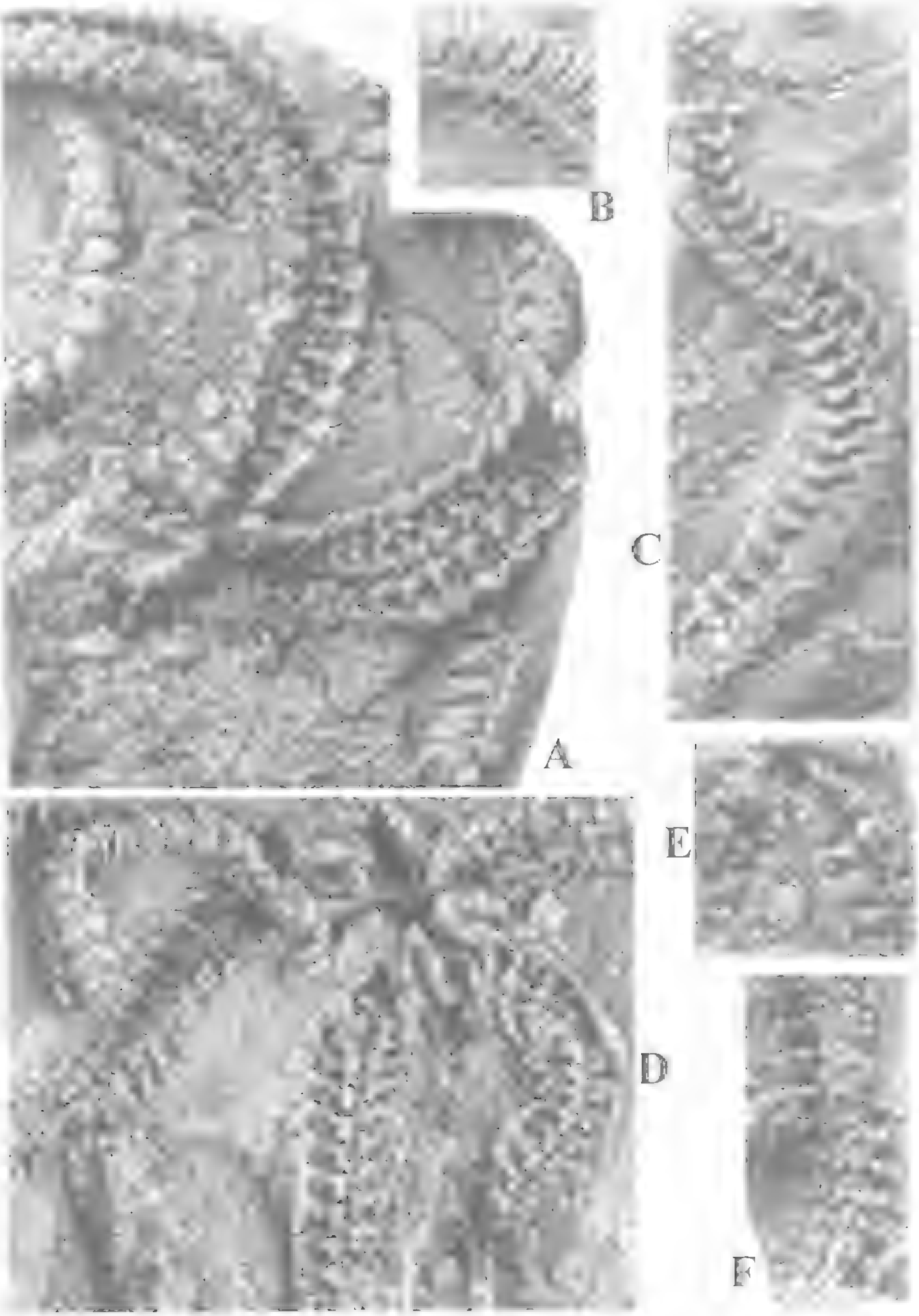



FIG. 55. *Stratasterstuckenbergi* (Rilett, 1971). A, ventral view showing madreporite, lateral and ventral spines on Adambb and plating in interradii in disc B4504 ×3.5. B, short section of arm showing long lateral spines on Adambb B4504 ×3.5. C, section of an arm showing spines on Adambb B4504 ×3.5. D, ventral view B4504 ×3.5. E, closeup of madreporite B4504 ×3.5. F, short section of an arm showing ventral spines on left and lateral spines on right B4504 ×3.5.

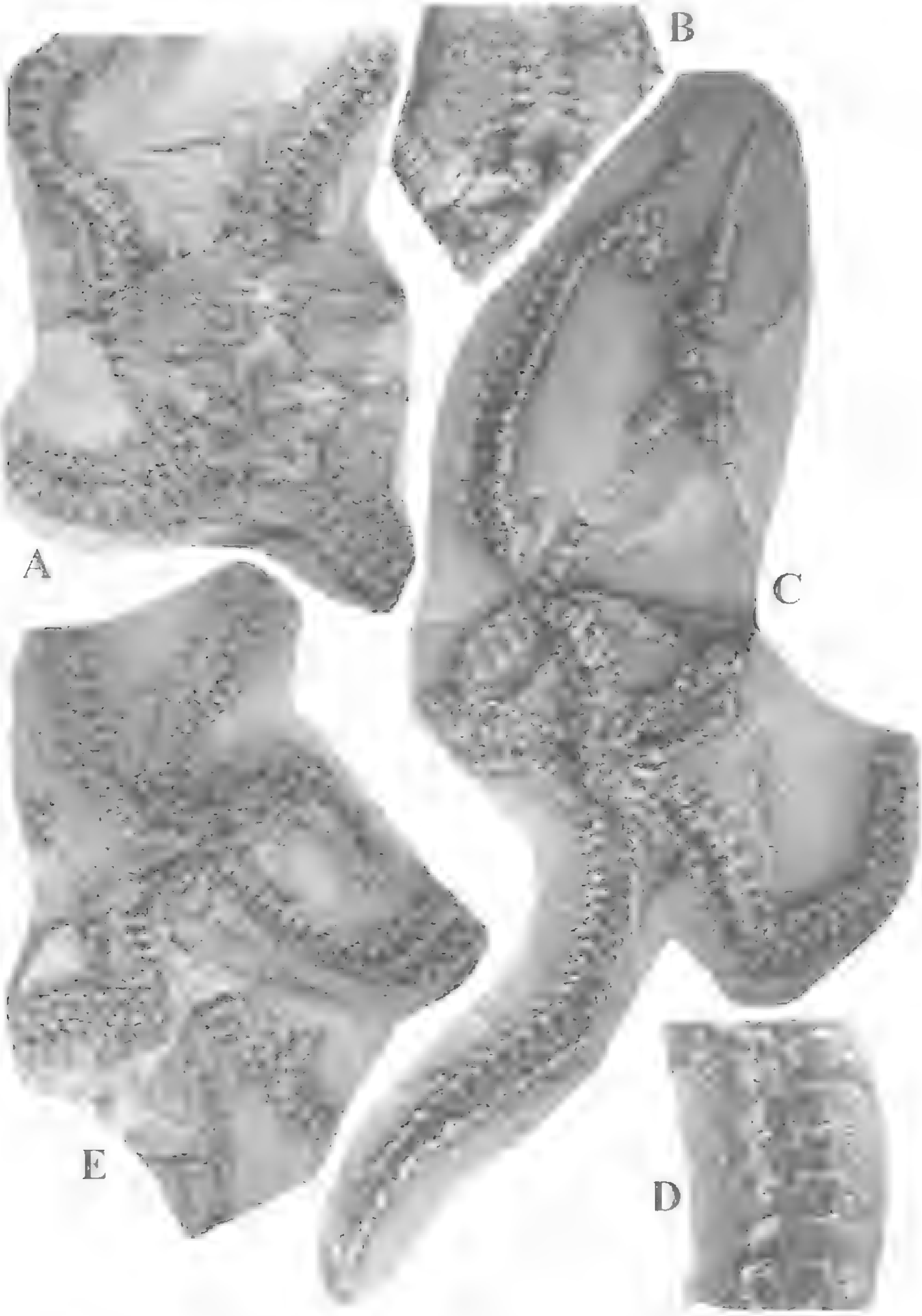



FIG. 56. *Strataster stuckenbergi* (Rilett, 1971). A, dorsal view of individual on back of type slab NM83 ×3 (figured by Rilett, 1971, Fig. 4). B, enlargement of part of disc showing spines on interradius B4504 ×3.4. C, ventral view of holotype showing the medial dorsal spine rows in several places NM type 1550 ×2.5. D, enlargement of upper arm in C in ventral view showing Adambb on both sides with ventral spines and at left the dorsal medial spine row ×5. E, ventral view of individual on back of NM831 ×2.5.

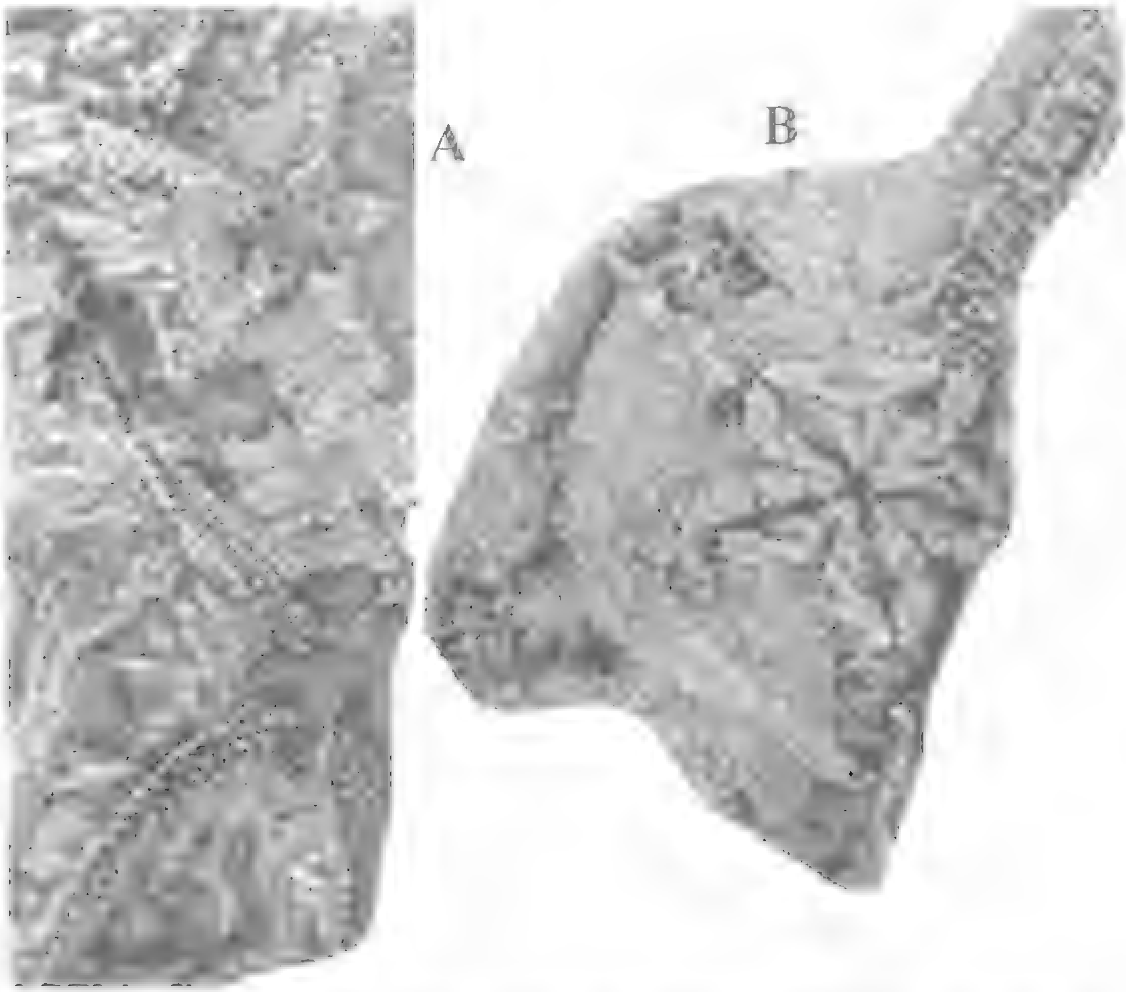



FIG 57. *Strataster* sp. A, dorsal view (upper) of disc with arms broken off at disc margin and ventral view (lower) of individual with disc not preserved SAM13475 ×3. B, dorsal view of disc and proximal arms with tori in place and suggestion of medial dorsal spine row on arm at 8 o'clock PRV 3231 ×5.

these ridges are parallel and further apart being near the proximal and distal edges of ambulacrals: still further distally (where ambulacrals subquadrate) the ridges not raised so, apart from the external integument, ambulacrals are then smooth, transversely convex and abut each other closely with only a narrow V-shaped cleft between plates. Junction of the 2 columns of ambulacrals is straight and capped by a line of prominent rounded dorsal spines on the free arm as far as the whip-like distal portion. Distally on the arms are papillae: skin a smooth tessellated pavement of small plates not extending over the entire adambulacral.

*Adambulacrals (or laterals).* One column of adambulacrals on each side of arms adjacent to ambulacrals. Each adambulacral gently convex (vertically), enclosing the arm laterally. Near its midheight is an adradial projection abutting the toe of the boot-shaped ridge on the ambulacral. Adradial margin of adambulacrals abutting ambulacrals along the outer edge of the floor of the podial basin. A shallow groove along the ventral edge, with 6 small pores at each of which is attached a curved (ventrally and distally) flattened spatulate spine; abradially on the distal margin (above the spatulate spines but in the same line as their groove) a pair of strong round tapering spines directed distally. Distally all spines are shorter, more slender, and

progressively fewer in number. Abradially they form a distinctive lateral column of plates closing off the abradial sides of the deep clefts between ambulacrals. Their outer or abradial margins are set en echelon with a large part of the distal face free and bearing the 2-3 distally directed circular-sectioned spines.

*Madreporite.* Interradial, ventral, smooth, gently convex, with a U-shaped aperture close to the plate margin on 3 sides and with the inside of the U slightly elevated. Within the interradius it is closer to the ambulacrum at the base of the U. Integument of the disc extends over the madreporite at least in the area at the top of the U.

*Disc.* External integument highly flexible, probably collagenous skin, covered with closely spaced papillae and widely distributed short circular or oval (in section) spines which are mostly broken off and represented by their smooth bases. Skin compressed down from the aboral side into the depressions among the mouthframe, extending over the entire dorsal disc, over the entire ventral interradii including the mouth frame but excepting the ambulacral grooves and mouth, also covering arms dorsally and laterally. Where the outer integument is not preserved, a mosaic of irregularly shaped flat plates is exposed. These have numerous projections which overlap, leaving some gaps; outer integument where preserved, with irregular depressions corresponding in size and probably position to these gaps and which have central spines. There is no differentiation of a marginal rim to the disc among these underlying plates. These plates are not joined by sutures but probably provided any structural rigidity in the disc.

*Mouthframe.* Large star-shaped, occupying about 1/2 disc diameter and formed mostly by modified 1st and 2nd ambulacrals. Although the aboral view in each available specimen is obscured by the outer integument, one specimen (Fig. 55A) shows 3 denticles in place on a torus; the denticles are best exhibited in a few oral views where 10 or more denticles are evident in a bundle. The 1st ambulacrals [MAP of most authors] are modified into radially elongate form, arranged in pairs interradially [1 from each arm], crossed transversely by well impressed groove for the nerve ring, and sutured distally in an oblique suture to the 2nd Amb (1st Amb of most authors). The groove for the water vascular ring, which runs around the mouthframe, does so across the 1st-2nd ambul- acral sutures as in other protasterids. In dorsal view 2nd ambulacrals are greatly elongate distally and extend over the top of at least 3rd and 4th ambulacrals. In ventral view 2nd ambulacral has rudimentary podial basin but also has adambulacral of 2nd and 3rd ambulacrals along its adradial margin. Face of 2nd ambulacral articulating with 3rd ambulacral is very high and concave. Adambulacrals on the adradial side of the enlarged 2nd ambulacral is clear in 2 specimens right into the vertical face of 1st ambulacrals at the edge of the mouth. There is the appearance that the adambulacral column moves from abradial to adradial relative to the ambulacral column but we think it more likely that they move further ventrally as well so making the change of orientation less dramatic. Adambulacrals adjacent to 1st and 2nd ambulacrals retain their full complement of ventral spines.

REMARKS. This species would fit into *Taeniaster* among genera available in Spencer & Wright (1966) but Hotchkiss (1970) and Kesling & Le Vasseur (1971) discussed that genus and relatives at length and separated *Strataster* on the basis of the line of carinal spines on upper arm plates among other features. It is separated from *S. ohioensis* by the shape of the madreporite, length of ambulacrals along arm axis and numerous spines on disc dorsally.

**Strataster** sp.
(Fig. 57)

MATERIAL. SAM13476 and PRV3231 from the Verstehoek Formation on hill on S side of farm Riet Rivier (Grootrivier) at N end of Ceres Division on Wupperthal Road.

REMARKS. This material is referred to *Strataster* based on the bases of middorsal spines (Fig. 57B, arm at 8 o'clock), the very strong dorsal transverse ridges on ambulacrals, shape of the boot-shaped ridges in ventral view and structure of the mouth frame. However, the lack of detail of dorsal integument which is apparently a tessellated pavement of irregular plates giving a smooth surface, no complete arm and no ventral view of the mouth frame prevent assignment to a known species. We prefer to retain these specimens in open nomenclature at present.

**Ophiuroid arms** indet. B
(Fig. 58B, C)

MATERIAL. B4546a-e from the Voorstehoek Formation (C2S2) at dieVlakte.

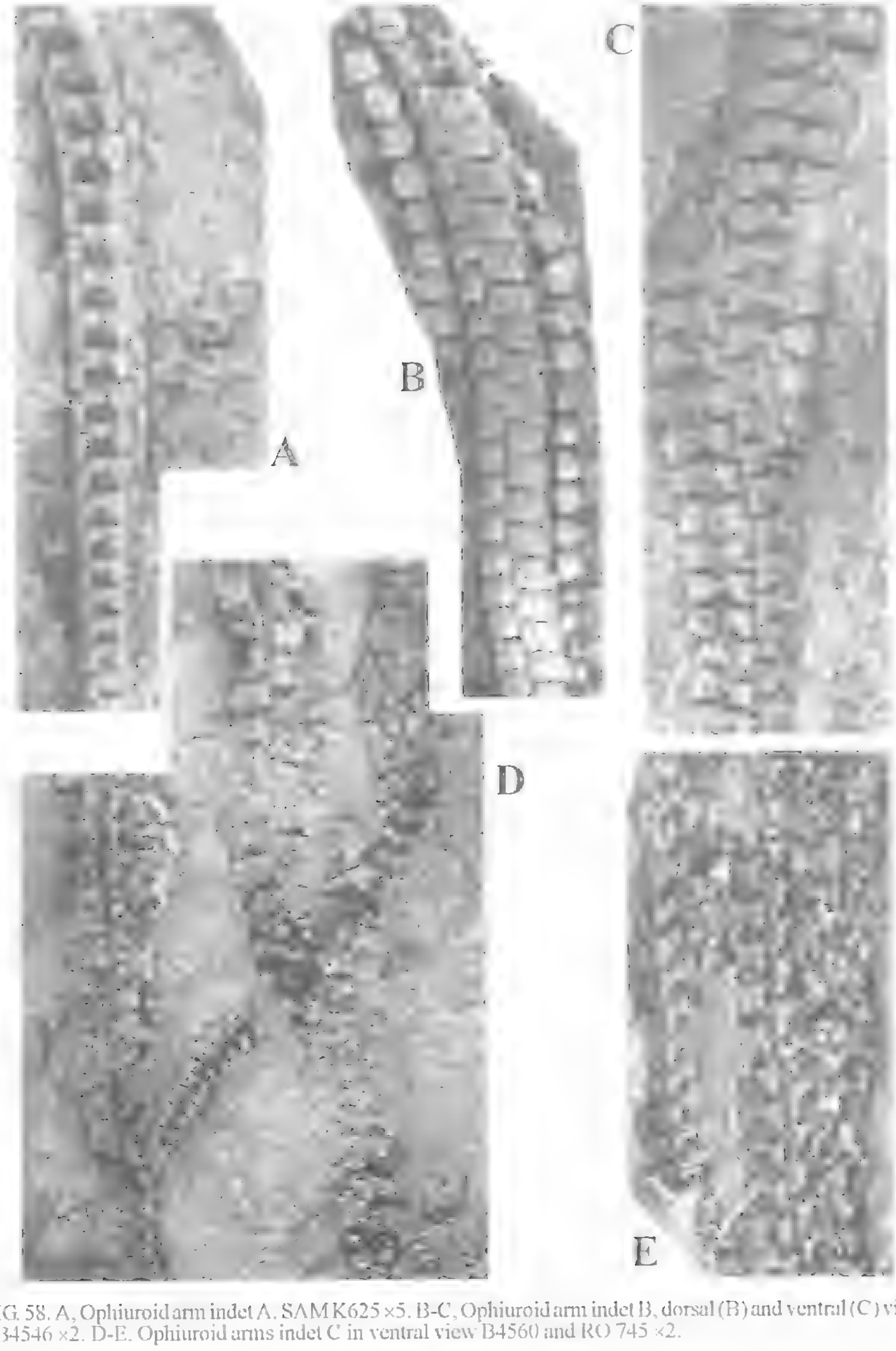



FIG. 58. A, Ophiuroid arm indet A. SAM K625 ×5. B-C, Ophiuroid arm indet B, dorsal (B) and ventral (C) views B4546 ×2. D-E. Ophiuroid arms indet C in ventral view B4560 and RO 745 ×2.

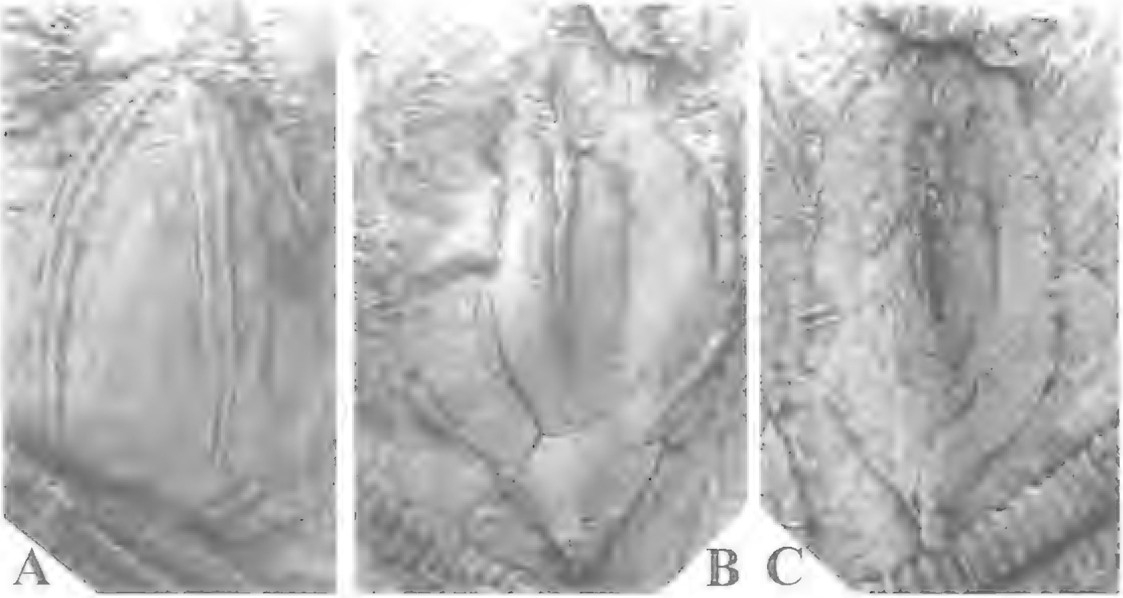



FIG. 59. *Pachyblastus dicki* Breimer & Macurda, 1972, all latex casts from external moulds of blastoid thecae in lateral view, all on one slab SAM K1068 ×2. A, holotype.

DESCRIPTION. Free arm fragments only available. Dorsal aspect with 2 columns of ambulacrals alternating along slightly zigzag arm axis and 2 lateral columns of club-shaped adambulacrals; ambulacrals closely sutured to each other within the column and across the arm axis, wider than long, smooth, weakly convex dorsal surface, with protruding obtusely angular adradial margin and concave abradial margin; adambulacrals dorsally separated from ambulacrals by short distance (ad-ab) less than the width of ambulacrals in which are discernible circular holes at the concave abradial margin, subquadrate, dorsally convex, about 1/2 width of adjacent ambulacral.

Ventral aspect with discrete narrow ambulacral channel and wide shallow ambulacral groove; ambulacrals boot-shaped, with attenuated toe sutured to opposing adradial projection on adambulacral; adambulacral greatly expanded abradially, not obviously bearing any spines; podial basins small in relation to size of surrounding plates, shared by 2 succeeding ambulacrals and adjacent adambulacrals.

REMARKS. This arm structure is distinguished among the South African ophiuroids described here by the close suture rather than a cleft between successive ambulacrals dorsally. Only *Haughtonaster reedi* Rilett, 1971 is comparable in this respect but its adambulacrals are distinctly different both dorsally and ventrally. We are not aware of a comparable arm structure in any known ophiuroid but with the preservation of this specimen we are forced to retain it in open nomenclature.

**Ophiuroid arms** indet. C
(Fig. 58D, E)

MATERIAL. B4560 from Gydo Pass (C2S1) and RO745 from Gamkapoort 33° 18'S, 21° 38'E (C2S1).

DESCRIPTION. Incomplete and partly disarticulated arm fragments only.

*Dorsal.* Ambulacrals in 2 columns, alternating along arm axis, about twice as wide as long, closely sutured (without cleft) along column and to opposing column, smooth; adambulacrals not evident dorsally.

*Ventral.* Ambulacral channel narrow, deep. Ambulacrals with strong boot-shaped ridge having thick leg, with pit in the floor of podial basin into abradial side of ambulacral. Adambulacral with L-shaped ridge abutting against toe of ambulacral and of more or less uniform width or wider in lateral longitudinal part, bearing numerous short pointed lateral spines. Podial basin with small perforation through floor between ambulacral and adambulacral, shared on 2 ambulacrals and one adambulacral, wider than long.

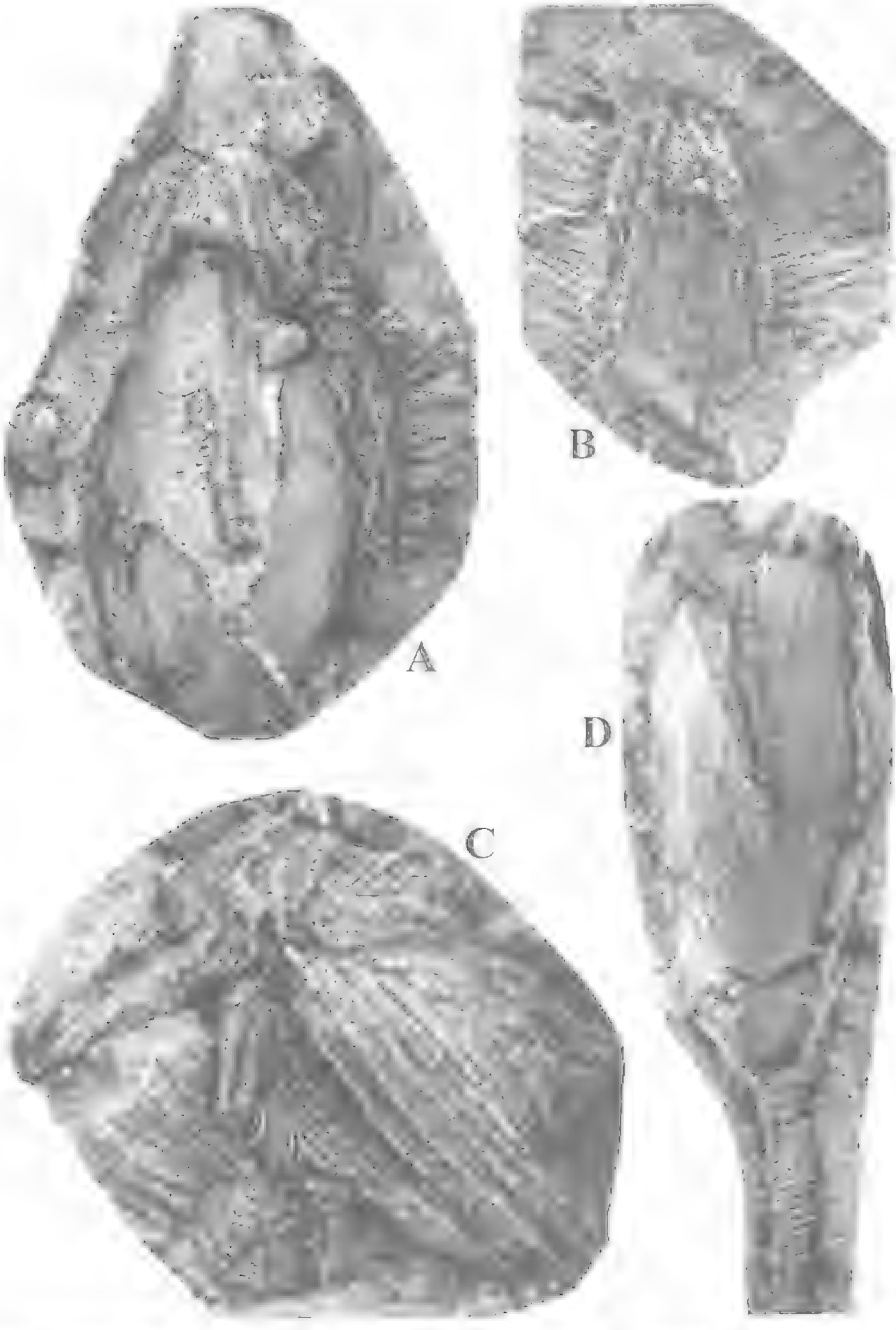



FIG. 60. *Pachyblastus dicki* Brenner & Macurda, 1972. A, lateral view of latex cast from part internal and part external (adorally) mould, B4590 ×2.2. B, lateral view of incomplete theca B4580 ×2.2. C, oblique dorsal view of theca B4597 ×2.7. D, lateral view of theca and proximal stem B4589 ×2.2.

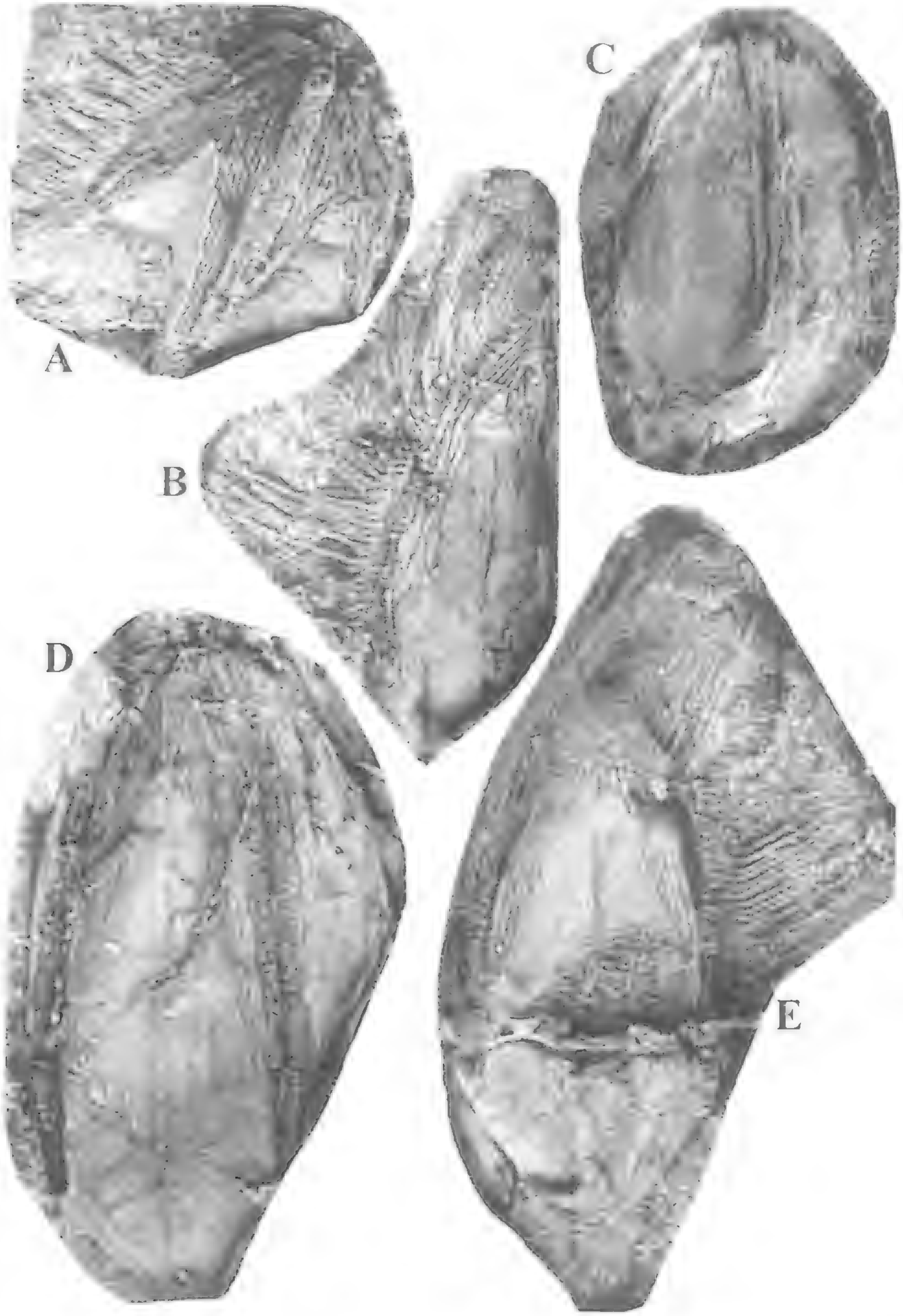



FIG. 61. *Pachyblastus dicki* Breimer & Macurda, 1972. A, oblique lateral view of incomplete theca B4597 ×2. B, lateral view of incomplete theca bearing long brachioles B4584 ×2. C, lateral view of theca B4521 ×1.7. D, lateral view of incomplete theca RO34a ×2.5. E, lateral view of theca with long brachioles in place and oral end missing B4570 ×2.5.

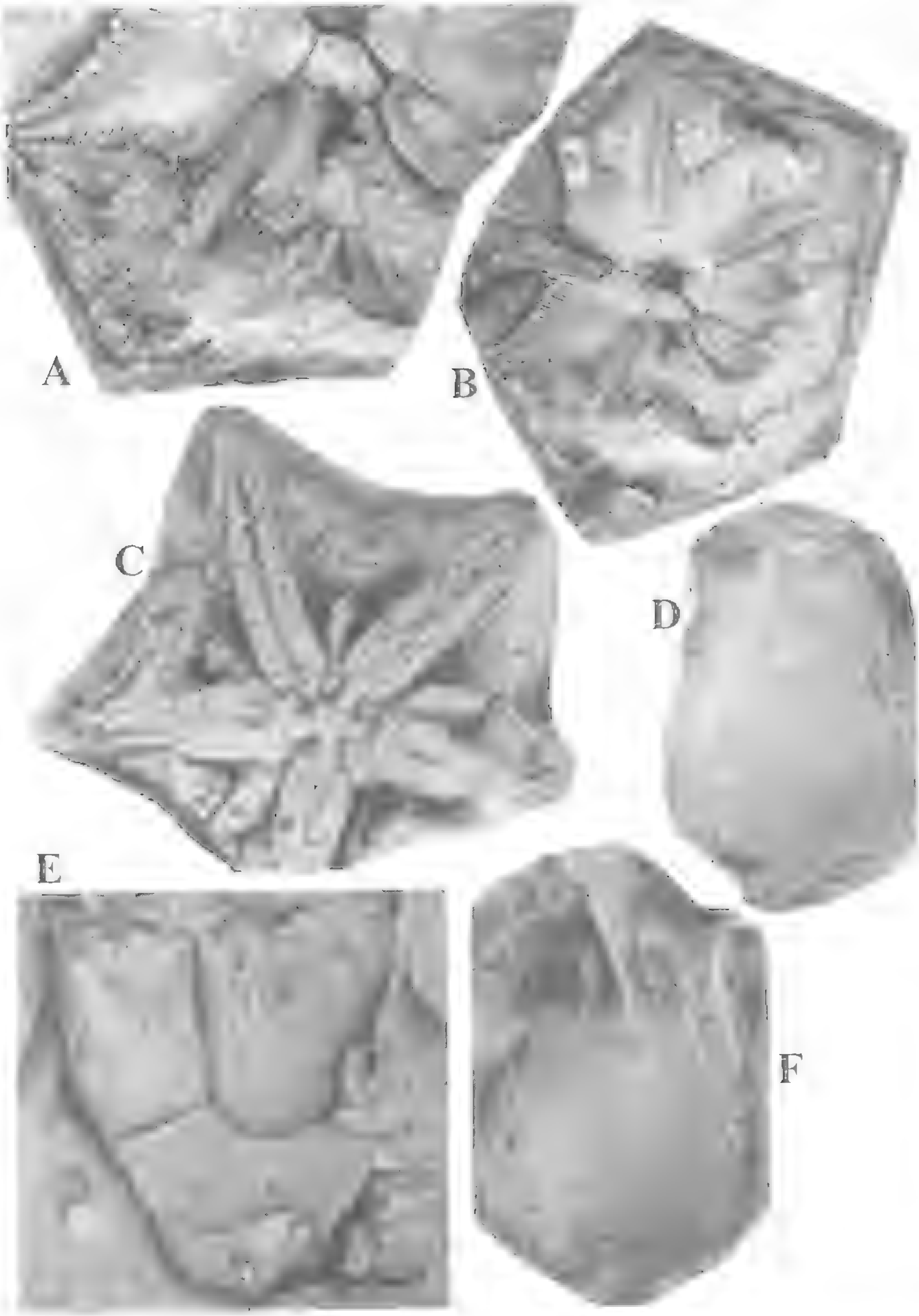



FIG. 62. *Brachyschisma oosthuizeni* Breimer & Macurda, 1972. A, B, interior view of oral surface of theca B4597 ×3.4 and ×4.7, respectively. Anal opening at 6 o'clock. C, oral view of holotype, a juvenile RO35(5) ×6. D, interior view of latex cast of radial SM A3045 ×5.2. E, lateral view of latex cast from juvenile theca RO 732(1) ×3.4. F, interior view of latex cast of radial RO E10 ×5.2.

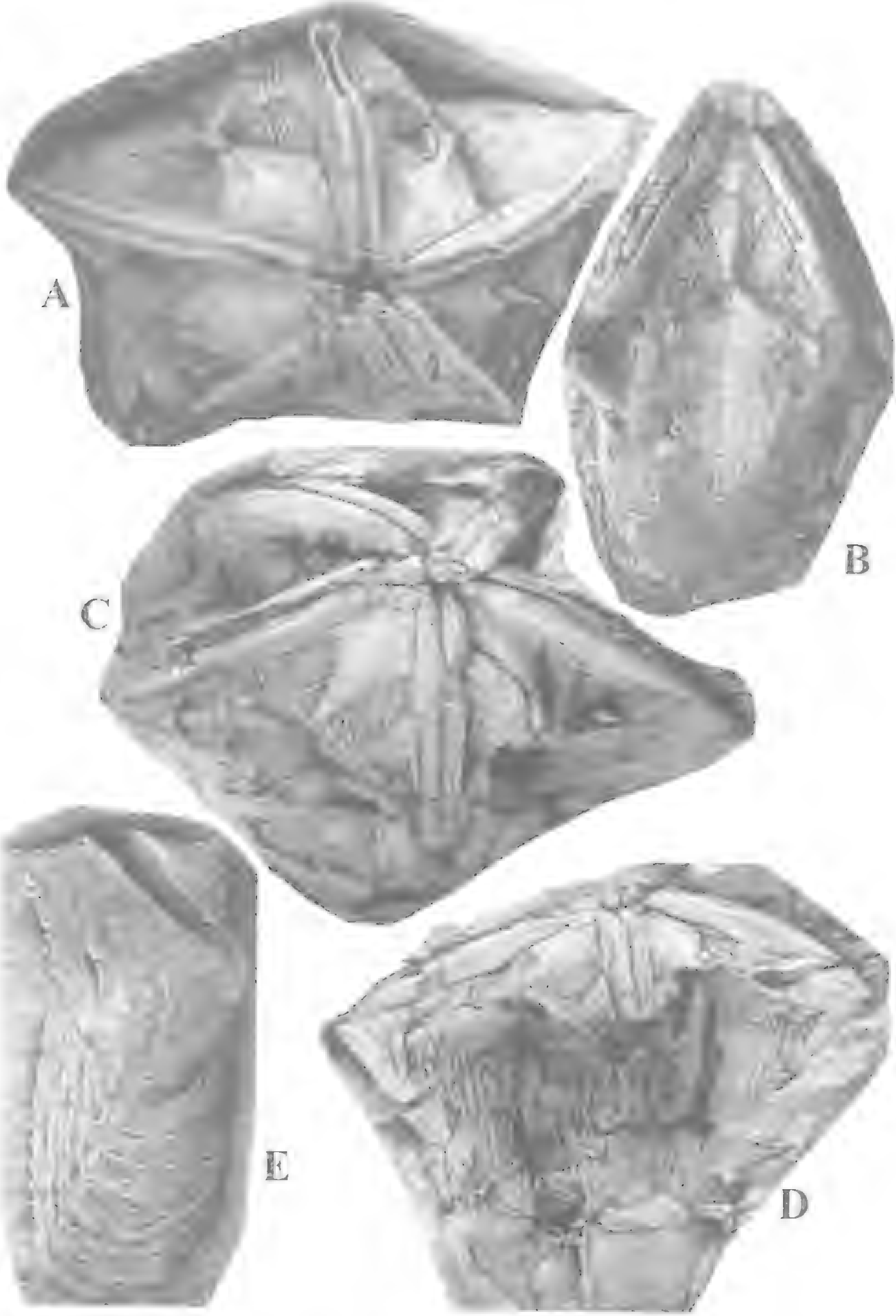


FIG. 63. *Brachyschisma oostheizeni* Breimer & Macurda, 1972. A, oral view of latex cast of theca with anal interarea at 6 o'clock B4596 ×2.5. B, lateral interradial view of latex cast of B4540 ×3.4. C,D, oblique oral and lateral views, respectively, of crushed B4595 ×2.5. E, lateral view of exterior of radial RO 35(6) ×2.5.

REMARKS. These poorly preserved specimens do not provide sufficient detail for identification but the wide ambulacrals and style of adambulacrals suggest affinity with the Cheiropterasteridae and the specimens could belong to *Hexuraster weitzi* Spencer, 1950a but we prefer to retain them in open nomenclature given their poor state of preservation.

Class BLASTOIDEA Say, 1825
Order FISSICULATA Jaekel, 1918
Family NYMPHAEOBLASTIDAE Wanner, 1940

**Pachyblastus** Breimer & Macurda, 1972

TYPE SPECIES. *Pachyblastus dicki* Breimer & Macurda, 1972.

**Pachyblastus dicki** Breimer & Macurda, 1972
(Figs 59-61)

MATERIAL. HOLOTYPE: SAMK1068 from the road from Hex Rivier Pass to Montagu Koo, 14km S of turnoff from N9, E of DeDoorns. B4519 from Theronsberg Pass near Ceres in the Waboomberg Formation, B4521, B4522 from Matroosberg, Stinkfontein (Hex River Pass). B4570, B4580, B4584, B4590 from the type locality. RO34a from Matroosberg, Worcester (Hex River Pass). 33°30'S, 19°49'E.

REMARKS. Breimer & Macurda (1972) and Macurda (1979, 1983) provided detailed descriptions of this monotypic genus based on the type material from South Africa and on Bolivian material of similar age in the Emsian. Breimer & Macurda (1972) noted that the type material, collected by Mr R.I. Dick was at that time in his private collection. In 1993 Mr Dick donated his collection to the Geological Survey of South Africa and it is now catalogued at the Regional Office at Bellville. Breimer & Macurda (1972) figured only 3 specimens on the type slab; this is a large slab and has many more specimens exposed on it, all as moulds. In this paper we have illustrated 3 latex casts (Fig. 59) from the moulds illustrated by Breimer & Macurda (1972) as well as latex casts of other individuals from the type and other slabs. These provide a more complete picture of the species but on no one of them are the anal deltoid plates clearly exposed.

The South African specimens figured herein differ from the Bolivian specimens (Macurda, 1979) by: 1, the very narrow median deltoid crest with hydrospire slits right up to the crest as opposed to a broader median zone without slits and bearing a broad low crest; 2, the side plates on the ambulacra concealing the lancet completely up to the adoral end; 3, a narrow ridge extending adorally from the adoral end of each ambulacrum (Fig. 60C) which may be due to preservation with the mouth closed. However, we would not suggest that these differences are sufficient to erect a new species and retain Macurda's concept of the species.

Family OROPHOCRINIDAE Jaekel, 1918

**Brachyschisma** Reimann, 1945

TYPE SPECIES. *Codaster corrugatus* Reimann, 1935 from the Middle Devonian of New York; by original designation.

**Brachyschisma oostheizeni**
Breimer & Macurda, 1972
(Figs 62, 63)

MATERIAL. HOLOTYPE: RO35 (Breimer & Macurda, 1972, pl. 6, fig. 3) from Gamkaskloof, Prince Albert (33°20'45"S, 21°47'30"E (C2S1). SMA3045 (Breimer & Macurda, 1972, pl. 6, fig. 13) from a road cutting between De Doorns and Triangle (Hex River Pass). RO732 (Breimer & Macurda, 1972, pl. 6, fig. 10), RO734 from Gamkapoort, Prince Albert, 33°18'S, 21°38'E (C2S1). ROE10 from Damascus, Prince Albert, 33°17'15"S, 21°55'45"E (C2S1). B4540 from Hex River Pass (C2S1). B4595, 4596 from Gydo Pass and Vleiland (C2S1), respectively. SAM13463, SAMK1026 from Koudeveldberg. SAM3376 from Laken Vlei, Ceres (C2S1).

DESCRIPTION. The following descriptive notes are additional to the accurate and detailed description of Macurda (1983: 80-81) or reflect the availability of much larger individuals and thus indications of changes with growth. Deltoid median radial crest most prominent in juveniles (e.g. holotype), becoming lower and broader relative to plate size with growth, higher distally at oral end of RR suture. Macurda (1983:81) gave measurements of a deltoid from the holotype whereas the following measurements are from a large specimen (Fig. 63A): L.: 10mm; Gr.Ad.W.: 1.2mm; Min.W.: 1.2mm; Gr.Ab.W.: 3.8mm; Deltoid lip 1/5 as long as deltoid body. Small specimens with 5-8 hydrospires per group whereas large specimens have up to 19 per group.

Anal deltoids 3, super-, sub- and hypodeltoid. Superdeltoid bordering oral opening, extending distally to tips of lancets, widest distally. Anal opening elliptical, elongate in radial direction. Subdeltoid horseshoe-shaped around proximal part of anal opening, with unequal limbs on either side of anal opening; with limb on D side shorter and narrower than that on C side, lacking hydrospires and not reaching radial but rather

abutting hypodeltoid; with limb on C side abutting radial and sharing with it a greatly reduced (for a large specimen) group of 6-8 hydrospires. Hypodeltoid disarticulated and not available on the latex (Fig. 62A) but space left by it approximately pentagonal and forming distal margin of anal opening (this margin is thus uncertain).

Hydrospire groups 9, absent from D side of anal interarea but present on C side.

REMARKS. The description given by Breimer & Macurda (1972) and Macurda (1983) was detailed and valid and is not repeated herein. Macurda (1983: 81) remarked that generic assignment could not be definite without knowledge of the anal deltoids. The anal deltoids are clear on the internal mould figured herein (Fig. 62A, B) and confirm the assignment to *Brachyschisma* while the larger specimens dealt with herein agree with Macurda's (1983) observation that *Brachyschisma* is the only comparable Devonian blastoid.

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## LITERATURE CITED

AUSICH, W.I. 1986. Early Silurian Rhodocrinitacean crinoids (Brassfield Formation, Ohio). Journal of Paleontology 60: 84-106.

1987. Brassfield Compsocrinina (Lower Silurian crinoids) from Ohio. Journal of Paleontology 61: 552-562.

BATHER, F.A. 1890. British fossil crinoids. II. The classification of the Inadunata Fistulata (cont'd). Annals and Magazine of Natural History, series 6, 5: 373-388.

BECKER, G., BLESS, J.M. & THERON, J.N. 1994. Malvinokaffric ostracods from South Africa (Southern Cape; Bokkeveld Group, Devonian). Courier Forschungs-Institut Senckenberg 169: 239-259.

BILLINGS, E. 1858. On the Asteriadae of the Lower Silurian rocks of Canada. Geological Survey of Canada, Figures and Descriptions of Canadian Organic Remains, decade 3: 75-85.

BJORK, P.R., GOLDBERG, P.S. & KESLING, R.V. 1968. Mouth frame of the ophiuroid *Onychaster*. Contributions from the Museum of Paleontology, University of Michigan 22: 45-60.

BLAKE, D.B. & GUENSBURG, T.E. 1989. Two new multiarmed Paleozoic (Mississippian) asterids (Echinodermata) and some paleobiologic implications. Journal of Paleontology 63: 331-340.

BOUCOT, A.J. 1971. Malvinokaffric Devonian marine community distribution and implications for Gondwana. Anais da Academia Brasileira de Ciencias 43 (supplement): 23-49.

BOUCOT, A.J., JOHNSON, J.G. & TALENT, J.A. 1969. Early Devonian brachiopod zoogeography. Special Papers of the Geological Society of America 119: 1-106.

BREIMER, A. 1962. A monograph on Spanish Palaeozoic Crinoidea. Overdruk uit Leidse Geologische Mededelingen 27: 1-189.

BREIMER, A. & MACURDA, D.B. 1972. The phylogeny of the fissiculate blastoids. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde, Eerste Reeks 26(3): 1-390.

BRONN, H.G. 1848. Index palaeontologicus oder Ubersicht der bis jetztbekannten fossilen Organismen, unter Mitwirkung der Herren Professor H.R. Göppert und H. von Meyer: Handbuch einer Geschichteder Natur 3, Abt. 1 (1,2), part 3, A. Nomenclator palaeontologicus. 1381p. (Schweizerbart: Stuttgart).

CLARKE, J.M. 1913. Fosseis devonianos do Paraná. Monographias do Servico Geologico e Mineralogico do Brasil 1: 1-353.

CORSTORPHINE, G.S. 1897. Report of the Acting Geologist for the year 1897. Report of the Geological Commission of the Cape of Good Hope 1897: 3-43.

DONOVAN, S.K. & CLARK, N.D.L. 1992. An unusual crinoid columnal morphospecies from the Llandovery of Scotland and Wales. Palaeontology 35: 27-35.

FOLLMANN, O. 1887. Unterdevonische Crinoiden. Verhandlungen des Naturhistorischen Vereines der preussischen Rheinlande, Westfalens und des Reg.-Bezirks Osnabrück 44: 113-138.

FREST, T.J. & STRIMPLE, H.L. 1981. New camerate crinoids from the Silurian of North America. Journal of Paleontology 55:639-655.

GOLDFUSS, G.A. 1848. Ein Seestern aus der Grauwacke. Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande 5: 145-146, 5pl.

GOLDRING, W. 1923. The Devonian crinoids of the State of New York. Memoirs of the New York State Museum 16: 1-670.

1954. Devonian crinoids: new and old, II. New York State Museum Circular 37: 1-51.

HAECKEL, E.H. 1866. Allgemeine Entwickelungsgeschichte der Organismen. In Haeckel, E. General Morphologie der Organismen. Vol. 2. 160p. (Berlin).

HALL, J. 1858. Report of the Geological Survey of Iowa, embracing the results of investigations made during portions of the years 1855, 1856, and 1857. Palaeontology of Iowa 1(2): 473-724. (Geological Survey of Iowa).

1879. The fauna of the Niagara Group in central Indiana. Annual Report of the New York State Museum of Natural History 28: 99-199.

HARPER, J.A. 1985. A new look at *Eugasterella logani* (Hall, 1868) (Stellaroidea:Ophiuroidea) from the Middle Devonian of New York State. Annals of the Carnegie Museum 54: 357-373.

HAUDE, R. 1995. Lower Devonian echinoderms from the Precordillera (Argentina). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 197: 37-86

1999. Der - verzögerte - Ersatz eines Homonyms: *Marginaster* Haude, 1995. Neues Jahrbuch für Geologie and Paläontologie Monatschefte 1999: 3p.

HILLER, N. & THERON, J.N. 1988. Benthic communities in the South African Devonian. Canadian Society of Petroleum Geologists Memoir 14: 229-242.

HINDE, G.J. 1885. Description of a new species of crinoids with articulating spines. Annals and Magazine of Natural History, series 5, 15: 157-173.

HOTCHKISS, F.H.C. 1970. North American Ordovician Ophiuroidea, the genus *Taeniaster* Billings, 1858 (Protasteridae). Proceedings of the Biological Society of Washington 83: 59-76.

1976. Devonian ophiuroids from New York State: reclassification of *Klasmura*, *Antiquaster*, and *Stenaster* into the suborder Scalarina nov., Order Stenurida. Bulletins of the New York State Museum 425: 1-39.

1993. A new Devonian ophiuroid (Echinodermata: Oegophiurida) from New York State and its bearing on the origin of ophiuroid upper arm plates. Proceedings of the Biological Society of Washington 106: 63-84.

1995. Loven's Law and adult ray homologies in echinoids, ophiuroids, edrioasteroids, and an ophiocistioid (Echinodermata: Eleutherozoa). Proceedings of the Biological Society of Washington 108: 401-435

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3(1): 1-128.

JELL, P.A. 1997. Early Carboniferous ophiuroids from Crawfordsville, Indiana. Journal of Paleontology 71: 306-316.

1999. Silurian and Devonian crinoids from central Victoria. Memoirs of the Queensland Museum 43: 1-114.

KESLING, R.V. 1972. *Strataster devonicus*, a new brittle-star with unusual preservation from the Middle Devonian Silica Formation of Ohio. Contributions from the Museum of Paleontology, University of Michigan 24: 9-15.

KESLING, R.V. & LE VASSEUR, D. 1971. *Strataster ohioensis*, a new early Mississippian brittle-star, and the paleoecology of its community. Contributions from the Museum of Paleontology, University of Michigan 23: 305-341.

KESLING, R.V. & CHILMAN, R.B., 1975. Strata and megafossils of the Middle Devonian Silica Formation. Papers in Paleontology from the Museum of Paleontology, University of Michigan 8: 5-123, 153-172.

KIER, P.M., 1952. Echinoderms of the Middle Devonian Silica Formation of Ohio. Contributions from the Museum of Paleontology, University of Michigan 10: 59-81.

1958. Infrabasals in the crinoid *Opsiocrinus* Kier. Contributions from the Museum of Paleontology, University of Michigan 13: 201- 206.

KIRK, E. 1934. *Corynecrinus*, a new Devonian crinoid genus. Proceedings of the U.S. National Museum 83(2972): 1-7.

KNOD, R. 1908. Devonische Faunen Boliviens. Neues Jahrbuch für Mineralogie, Geologie und Palaontologie, Beil. Band 25: 493-600.

KOZLOWSKI, R. 1923. Faune dévonienne de Bolivie. Annales de Paléontologié 12: 1-112.

LEHMANN, W.M. 1957. Die Asterozoen in den Dachschiefern des rheinischen Unterdevons. Abhandlungen des Hessischen Landesamtes für Bodenforschung 21: 1-160, 55 pls.

LYON, S.S. 1857. Palaeontological Report. Geological Report of Kentucky 3: 467-497.

MACURDA, D.B. 1979. The Devonian blastoids of Bolivia. Journal of Paleontology 53: 1361-1373.

1983. Systematics of the fissiculate Blastoidea. Papers in Paleontology from the Museum of Paleontology at the University of Michigan 22: 1-291.

McINTOSH, G.C. 1979. Abnormal specimens of the Middle Devonian crinoid *Bactrocrinites* and their effect on the taxonomy of the genus. Journal of Paleontology 53: 18-28.

1983. Review of the Devonian cladid inadunate crinoids: Suborder Dendrocrinina. PhD Thesis, University of Michigan.

1986. Phylogeny of the dicyclic inadunate crinoid Order Cladida. Abstr. 4th North American Palaeontological Convention.

McINTOSH, G.C. & BRETT, C.E., 1988. Occurrence of the cladid inadunate crinoid *Thalamocrinus* in the Silurian (Wenlockian) of New York and Ontario. Contributions to the Life Sciences from the Royal Ontario Museum 149: 1-17.

MILLER, S.A. 1889. North American geology and paleontology. (Western Methodist Book Concern: Cincinnati).

MILLER, S.A. & GURLEY, W.F.E. 1895. Description of new species of Palaeozoic Echinodermata. Illinois State Museum Bulletin 6: 1-62.

MOORE, R.C. 1962. Ray structures of some inadunate crinoids. University of Kansas, Paleontological Contributions, Echinodermata, Article 5: 1-47.

MOORE, R.C. & JEFFORDS, R.W., 1968. Classification and nomenclature of fossil crinoids based on studies of their columns. University of Kansas, Paleontological Contributions, Echinodermata, Article 9(46): 1-86.

MOORE, R.C., LANE, N.G. & STRIMPLE, H.L., 1978. Order Cladida Moore & Laudon, 1943. Pp. T578-T759. In Moore, R.C. & Teichert, C. (eds) Treatise on invertebrate paleontology, Part T, Echinodermata 2 (Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas).

MOORE, R.C. & LAUDON, L.R., 1943. Evolution and classification of Paleozoic crinoids. Geological Society of America Special Paper 46: 1-153.

MOORE, R.C. & TEICHERT, C. (eds) 1978. Treatise on invertebrate paleontology, Part T, Echinodermata 2, Crinoidea. 3 vols. (Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas).

OOSTHUIZEN, R.D.F. 1984. Preliminary catalogue and report on the biostratigraphy and palaeogeographic distribution of the Bokkeveld fauna. Transactions of the Geological Society of South Africa 87: 125-140.

PERRIER, E. 1881. Description sommaire des espèces nouvelles d'astérias. Bulletin of the Museum of Comparative Zoology, Harvard University 9: 1-31.

REED, F.R.C. 1904. Mollusca from the Bokkeveld Beds. Annals of the South African Museum 4: 239-274.

1906. New fossils from the Bokkeveld Beds. Geological Magazine, Decade 5, 3: 301-310.

1907. Fauna of the Bokkeveld beds. Geological Magazine, Decade 5, 4: 166-171, 222-232.

1925. Revision of the fauna of the Bokkeveld Beds. Annals of the South African Museum 22: 27-225.

REIMANN, I.G. 1935. New species and some new occurrences of Middle Devonian blastoids. Bulletin of the Buffalo Society of Natural History 17: 23-45.

1945. New Devonian blastoids. Bulletin of the Buffalo Society of Natural Sciences 19(2): 22-42.

RENNIE, J.V.L. 1936. On *Placocystella*, a new genus of cystids from the Lower Devonian of South Africa. Annals of the South African Museum 31: 269-275.

RILETT, M.H.P. 1971. Two new fossil ophiuroid species from the Bokkeveld Series, near Ceres, Cape Province. Annales of the Natal Museum 21: 29-35.

ROEMER, F. 1863. Neue Asteriden und Crinoiden aus devonischem Dachschiefer von Bundenbach bei Birkenfeld. Palaeontographica 9:143-152, pls 23-29.

ROSSOUW, P.J., 1933. On the geology of Weltevreden, Prince Albert district, with a diagnosis of an ophiuroid, *Ophiurites* sp. Transactions of the Geological Society of South Africa 36: 73-76.

RUEDEMANN, R. 1916. Palaeontologic contributions from the New York State Museum. New York State Museum Bulletin 189: 1-225.

RUST, I.C. 1973. The evolution of the Palaeozoic Cape Basin, southern margin of Africa. Pp. 247-276. In Nairn, A.E.M. & Stehli, F.G. (eds) The ocean basins and margins, 1. The South Atlantic. (Plenum: New York).

RUTA, M. & THERON, J.N. 1997. Two Devonian mitrates from South Africa. Palaeontology 40: 201-243.

SALTER, J.W. 1856. Description of Palaeozoic Crustacea and Radiata from South Africa. Transactions of the Geological Society of London 7: 215-224.

SANDBERGER, F. 1852. Uber einige paläozoische Versteinerungen des Cap-Landes. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefactin-Kunde, Abhandlungen A 1852: 581-585.

SCHMIDT, W.E. 1934. Die Crinoideen des Rheinischen Devons. Teil 1: Die Crinoideen des Hunsrückschiefers. Abhandlungen der Preussischen Geologischen Landesanstalt 163: 1-149.

1941. Die Crinoideen des Rheinischen Devons. Abhandlungen der Reichsstelle für Bodenforschung, Neue Folge 182: 1-253, pls 1-26.

SCHÖNDORF,F. 1910. Paläozoische Seesterne Deutschlands. 2. Die Aspidosomatiden des deutschen Unterdevon. Palaeontographica 57: 1-66.

SCHUCHERT, C. 1914. Stellaroidea palaeozoica. Pp.1-53. In Frech, F. (ed.) Fossilium Catalogus 1: Animalia Part 3. (W. Junk: Berlin).

1915. Revision of Paleozoic Stelleroidea with special reference to North American Asteroidea. United States National Museum Bulletin 88:1-311, pls 1-38.

SCHWARZ, E.H.L. 1906. South African Palaeozoic fossils. Records of the Albany Museum 1: 347-404.

SHARPE, D. & SALTER, J.W. 1856. Description of Palaeozoic fossils from South Africa. Transactions of the Geological Society of London 7: 203-206.

SIMON, E. 1884. Note sur le groupe des *Microbothria*. Bulletin de la Societé du Zoologique 9: 313-317.
SMITH, A.B. & JELL, P.A. 1990. Cambrian edrioasteroids from Australia and the origin of starfishes. Memoirs of the Queensland Museum 28: 715-778.
SPENCER, W.K., 1914. British Palaeozoic Asterozoa. Part 1. Palaeontographical Society Monographs 1913: 1-56
1930. British Palaeozoic Asterozoa. Part 8. Palaeontographical Society Monographs 1928: 389-436.
1934. British Palaeozoic Asterozoa. Part 9. Palaeontographical Society Monographs 1933: 437-494.
1950a. A new brittlestar and an eurypterid from the Bokkeveld Strata. South African Journal of Science 46: 300-301.
1950b. Asterozoa and the study of Palaeozoic faunas. Geological Magazine 87:393-408.
SPENCER, W.K. & WRIGHT, C.W. 1966. Asterozoans. Pp. U4-U107. In Moore, R.C. (ed.). Treatise on invertebrate paleontology. Part U. Echinodermata 3(1). (Geological Society of America & University of Kansas Press: New York).
STEWART, G.A., 1940. Crinoids from the Silica Shale, Devonian, of Ohio. Ohio Journal of Science 40: 53-61.
STUKALINA, G.A., 1978. Cystoidea and crinoids. Trudy Institut Geologii i Geofiziki 397: 145-164.
TANKARD, A.J. & BARWIS, J.H. 1982. Wave-dominated deltaic sedimentation in the Devonian Bokkeveld basin of South Africa. Journal of Sedimentary Petrology 52: 959-974.
THERON, J.N. 1970. A stratigraphical study of the Bokkeveld Group (Series). Pp. 197-204. In Haughton, E.H. (ed.) Second International Gondwana Symposium, Proceedings and Papers (Council for Scientific and Industrial Research: Pretoria).
1972. The stratigraphy and sedimentation of the Bokkeveld Group. DSc Thesis, University of Stellenbosch.
THERON, J.N. & JOHNSON, M.R. 1991. Bokkeveld Group (including the Ceres, Bidouw and Traka Subgroups). Pp. 3-3 to 3-6. In Johnson, M.R. (ed.) Catalogue of South African Lithostratigraphic units. (South African Committee for Stratigraphy: Pretoria).
THERON, J.N. & LOOCK, J.C. 1988. Devonian deltas of the Cape Supergroup, South Africa. Canadian Society of Petroleum Geologists Memoir 14: 729-740.
THERON, J.N., BASSON, W.A. & HILL, R.S. 1995. Lithostratigraphy of the Gamka Formation (Bokkeveld Group). Lithostratigraphic series, South African Committee for Stratigraphy 29: 1-13.
THOM, G. 1830. Remarks on the geology of South Africa. South African Quarterly Journal 1: 269-271.
UBAGHS, G. 1978. Camerata. Pp. T408-T519. In Moore, R.C. & Teichert, C. (eds) Treatise on invertebrate paleontology, Part T, Echinodermata 2, Crinoidea. (Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas).
WACHSMUTH, C. & SPRINGER, F. 1880. Revision of the Palaeocrinoidea. Part 1. the families Ichthyocrinidae and Cyathocrinidae. Proceedings of the Academy of Natural Sciences of Philadelphia 1880: 226-378.
1886. Revision of the Palaeocrinoidea. Part 3, Section 2. Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions. Proceedings of the Academy of Natural Sciences of Philadelphia 1886: 64-226.
1897. The North American Crinoidea Camerata. Harvard College Museum of Comparative Zoology Memoir 20: 1-897, pls 1-83 (3 vols).
WANNER, J. 1940. Neue Blastoideen aus dem Perm von Timor (mit einem Beitrag zur Systematik der Blastoideen). Geological Expedition to the Lesser Sunda Islands under the leadership of H.A. Brouwer 1: 217-277.
WILLIAMS, H.S. 1883. On a crinoid with movable spines (*Arthroacantha ithacensis*). American Philosophical Society Proceedings 21: 81-88.
WITHERS, R.B. & KEBLE, R.A. 1934. The Palaeozoic starfish of Victoria. Proceedings of the Royal Society of Victoria, new series 46: 220-249.

# CRINOIDS, A BLASTOID AND A CYCLOCYSTOID FROM THE UPPER DEVONIAN REEF COMPLEX OF THE CANNING BASIN, WESTERN AUSTRALIA

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This first systematic treatment of echinoderms from the extensive Upper Devonian reef complex of the northern Canning Basin erects the Frasnian blastoid *Hyperoblastus buglensis* sp. nov. and crinoids *Codiacrinus nicolli* sp. nov., *Melocrinites solidus* sp. nov. and *Hexacrinites brownlawi* sp. nov. and the Famennian crinoids *Jaekelicrinus murrayi* sp. nov., *Playfordicrinus kellyensis* gen. et sp. nov., *Wacrinus caseyensis* gen. et sp. nov. and *W. millardensis* gen. et sp. nov., with *J. murrayi* first appearing at the very top of the Frasnian. These echinoderms which have affinities with Siberian and European faunas occur mainly in the fine, red, fore reef Virgin Hills Formation with numerous holdfasts (some directly onto algal mounds) suggesting they lived in this environment. While much disaggregated crinoidal material is found in the cleaner reefal limestones the only cup found is *Stylocrinus tabulatus* Goldfuss, 1839 in Frasnian fore reef talus slope Sadler Limestone in the Paddy's Valley area. In the same insoluble residue was a marginal cyclocystoid plate, the youngest record of the class. ☐ *Crinoids, blastoid, cyclocystoid, Upper Devonian, Canning Basin.*

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Crinoidal remains have been recognised in the Upper Devonian reef complexes of the Canning Basin by many workers since the earliest days of exploration. However, only Teichert (1949) applied any generic level taxonomy to Devonian crinoids from the basin. He listed *Storthingocrinus*? nov. sp. from the Frasnian *Manticoceras* Zone, the fauna of which he collected in the Bugle Gap and No. 10 Bore areas; we have not been able to recollect that crinoid genus in those areas and a search of the collections of the University of Western Australia failed to produce Teichert's specimen. However, it seems possible that Teichert's material could be the same as that attributed below to *Stylocrinus tabulatus* Goldfuss, 1839 from Frasnian Sadler Limestone just to the W of Bugle Gap in Paddy's Valley. Blastoids and cyclocystoids have not previously been described from the Basin.

This is the first paper to describe Devonian echinoderms from the Canning Basin and includes the first knowledge of Upper Devonian crinoids, blastoids or cyclocystoids from the Southern Hemisphere. It represents the results of fewer than 10 collecting trips encompassing a small percentage of the Basin's Devonian outcrop. Judging from the volume of disaggregated crinoidal material encountered at most localities and the area of Devonian outcrop yet to be investigated in detail for echinoderms it seems highly probable that a much larger Upper Devonian fauna than the <10 taxa reported here will ultimately be discovered.

## GEOLOGICAL SETTING

All the fossils described herein come from the late Frasnian to Famennian part of the Devonian reef complexes along the northern margin of the Canning Basin. A great deal has been written about the geology of these reefs but the major geological mapping of the area was provided by Playford & Lowry (1966). Taxonomic studies with consequent biostratigraphic inferences have addressed most fossil groups found therein, including corals (Hill & Jell, 1970), brachiopods (Veevers, 1959), sponges (Rigby, 1986), stromatoporoids (Cockbain, 1984), crustacea (Briggs & Rolfe, 1983) and fish (Long, 1991) among others. However, the most useful groups for biostratigraphy have been conodonts (Glenister & Klapper, 1966; Druce, 1976) and goniatites (Glenister, 1958; Becker et al., 1993; Becker & House, 1997) and it is through these 2 groups that we have attempted to place the crinoids in stratigraphic sequence (Table 1).

All except 2 taxa come from the Virgin Hills Formation, which is a red muddy carbonate deposited on the fore reef slope and in inter-reefal

| | Conodont Zones | *Stylocrinus tabulatus* | *Hyperoblastus buglensis* | *Hexacrinites brownlawi* | *Taxocrinus* sp. | *Codiacrinus nicolli* | *Playfordicrinus kellyensis* | *Jaekelicrinus murrayi* | *Melocrinites solidus* | *Forbesiocrinus* | *Bacrinus caseyensis* | *Bacrinus millardensis* | Catillocrinid | Localities |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Famennian | *trachyptera* | | | | | | | X | | | | | | NMVPL1950-56 |
| | *marginifera* | | | | | | | | | | X | X | | NMVPL1931 NMVPL1930 |
| | | | | | | | | X | | X | | | | NMVPL1930, NMVPL1939 |
| | *rhomboidea* | | | | | | X | X | | | | X | X | NMVPL1936, 1938, 1942 |
| | *crepida* | | | | | | | | | | | | | |
| | *P. triangularis* | | | | | | | X | | X | | | | NMVPL1929 |
| Frasnian | *linguiformis* | ? | X | X | X | X | | X | X | | | | | QML1029, QML1031 |
| | *gigas* | ? | | | | | | | | | | | | |
| | *A. triangularis* | ? | | | | | | | | | | | | |
| | *asymmetrica* | ? | | | | | | | | | | | | |

TABLE 1. Stratigraphic distribution of crinoids described, against international conodont biozonation taken from Talent et al., 1993; localities detailed in Appendix are listed against this conodont scale.

shallow basins. The formation includes a variety of lithofacies indicating numerous environmental changes and events. It is not the aim of this paper to go into the geological history of the area which can be gleaned from the numerous references mentioned above. Crinoid holdfasts occur in situ on a number of bedding surfaces, especially ones representing stillstands or transgressive periods when sedimentation rates were extremely slow. Crinoidal debris, including cups, is scattered throughout most horizons but is most abundant with the holfasts. The cup of only one species, *Stylocrinus tabulatus* Goldfuss, 1839, and a wide variety of stem debris are known from the Sadler Limestone which is a reef talus deposit representing a higher energy environment. Doubtless, crinoids were common on the reefs but were disarticulated after death. No doubt more will be found in the reef limestones especially where silicified faunas are etched free but at this stage our knowledge of them remains poor. The single marginal ossicle of a cyclocystoid found in the same insoluble residue as *S. tabulatus* cannot be generically assigned but its occurrence extends the range of the class which was previously unknown in strata younger than Eifelian (Europe).

## SYSTEMATICS

Material described herein is housed in the Museum of Victoria (NMVP), Queensland Museum (QMF), Australian Geological Survey Organisation (CPC) and Geological Survey of Western Australia (GSWA) and comes from localities (Appendix 1) catalogued in the Museum of Victoria (NMVPL) and Queensland Museum (QML). All the specimens are preserved as carbonate, probably original skeleton, in a muddy carbonate matrix. They are variously weathered and are photographed in this state after blackening with a monomolecular layer of colloidal graphite and whitening with ammonium chloride sublimate. Terminology follows Moore & Teichert (1978). Measurements are given as: length, parallel to the central axis; width, transverse to, but never cutting or joining the central axis; and depth, normal to, and may join the central axis.

Phylum ECHINODERMATA
Class BLASTOIDEA Say, 1825
Order SPIRACULATA Jaekel, 1918
Family HYPEROBLASTIDAE Fay, 1964

We follow the family concept of Waters & Horowitz (1993).

### **Hyperoblastus** Fay, 1961

TYPE SPECIES. (by original designation) *Pentremitidea preciosa* Reimann, 1945 (=*Pentremitidea filosa* Whiteaves, 1887) from the Middle Devonian of Ontario.

DIAGNOSIS. See Breimer & Dop, 1975.

### **Hyperoblastus buglensis** sp. nov.
(Figs 1-4)

ETYMOLOGY. From Bugle Gap.

MATERIAL. HOLOTYPE: QMF36161. PARATYPES: QMF36162-36168, 40357-40359. All from QML1031, on E side of Bugle Gap S of Wagon Pass.

DIAGNOSIS. Conical pelvis, low vault, pelvic angle c.70°, with 3 hydrospires per group; lancet concealed, with raised diamond-shaped adoral end, with sharp dorsal ridge.

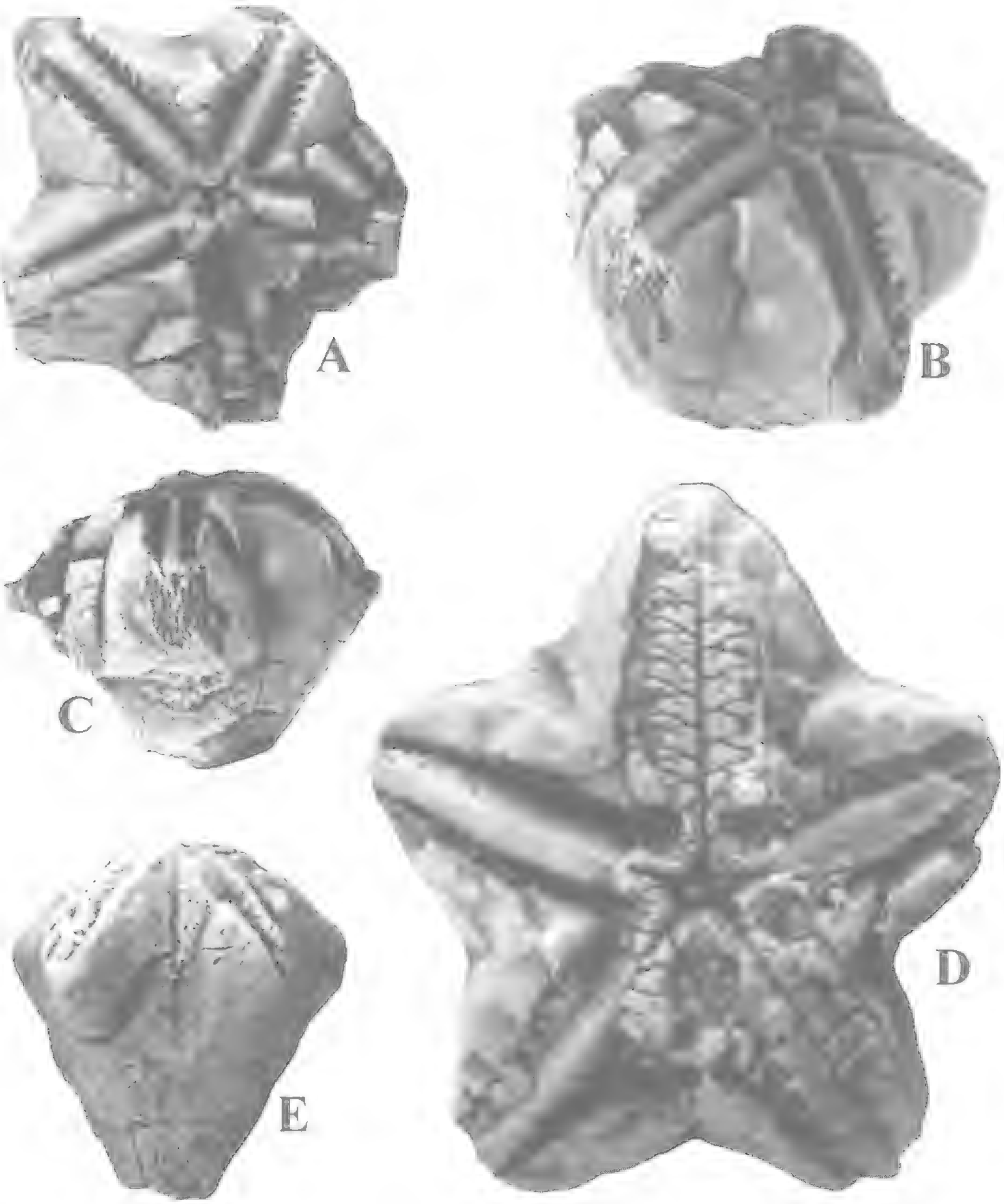



FIG. 1. *Hyperoblastus buglensis* sp. nov. all from QML1031. A-C, QMF36162, ×5. A, oral view showing fine pores from hydrospires. B, oblique oral view. C, lateral view of B ambulacrum showing hydrospire slits. D,E, oral and lateral views of QMF36161, ×12 and ×5, respectively.

DESCRIPTION. Cup smooth, up to 12mm long and 12mm wide at tips of ambulacra, conical, made up of conical pelvis with straight sides, capped by convex vault (Figs 1E, 3H); vault: pelvis = 1:2; pelvic angle 65-72° (av. 68°; N=7) Cross section at greatest width pentastellate. Basals 3, normally arranged, with 2 large hexagonal and one smaller pentagonal azygous. Radials 5, up to 8mm high, with convex radial fronts in lateral view; RD axis less than RB axis

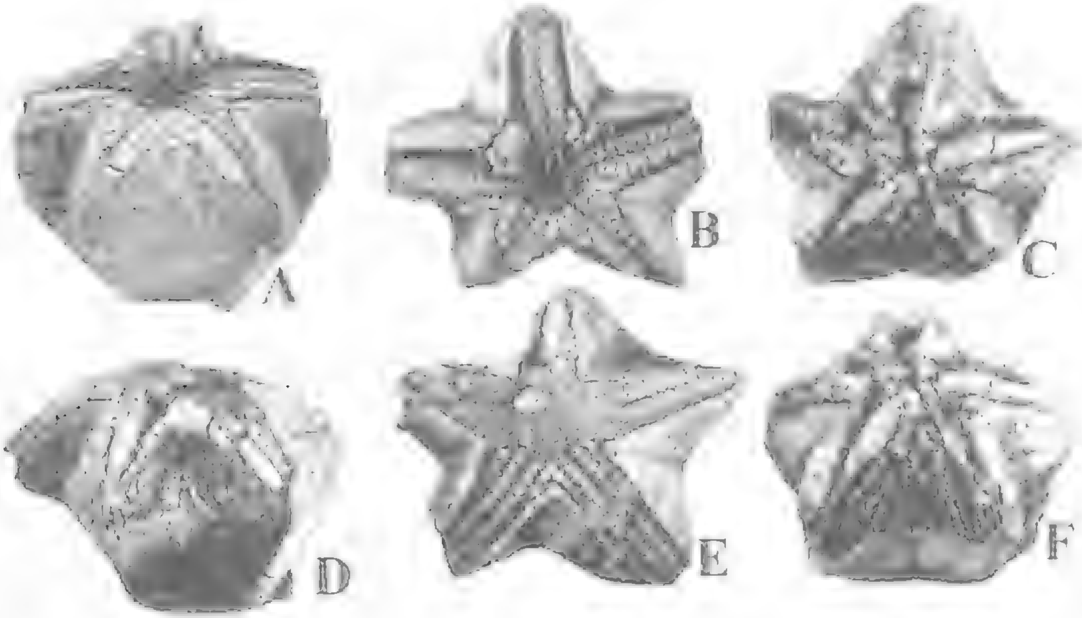



FIG 2. *Hyperoblastus buglensis* sp. nov. all from QML1031. A,B, QMF40357, ×6. A, oblique posterior view. B, oral view. C,F, QMF40358, ×6. C, oral view. F, oblique posterior view. D,E, QMF40359, ×4. D, oblique posterior view, E, oral view.

at all sizes; RD front straight. Deltoids concealed by radials and ambulacral side plates except for narrow adoral lip, separated from radials by suture highly oblique to radial surface (Fig. 1A,D); adoral lips of deltoids contiguous as peristome. Spiracles 4 plus slightly larger anispiracle, each descending into deltoid at very low angle to external surface dividing into 2 at depth within deltoid but deltoid septum only evident in weathered specimens, connecting into the hydrospire canals on either side of the lancet. Anal deltoids 3, a superdeltoid, a subdeltoid and a hypodeltoid (Fig. 4C); superdeltoid slightly wider than other deltoid lips, sutured aborally and laterally to raised anterior diamond of lancet. Lancet concealed except adoral end; prominent raised diamond-shaped adoral end sutured to aboral lateral ends of each deltoid lip, forming lateral margins to spiracles, crossed by radial median groove, abutting most adoral side plates; rest of lancet with obtuse but sharp upper keel, with row of uniform shallow concavities along each upper surface accommodating the inner side plates and alternating with similar concavities in the radial adjoining each ambulacrum accommodating the outer side plates. Side plates in 2 alternating columns on each side of each ambulacrum, up to 15 per column; inner side plates larger and reaching to outer margin of ambulacrum except in adoral 1/3 but triangular outer side plates never reaching midline of ambulacrum. Side plates filling grooves between lancet and radials; access to hydrospires via a series of pores at outer margin of ambulacrum. Hydrospire groups 10, extending some distance into coelomic cavity from sides of ambulacra, 3 hydrospires per group, no hydrospire plate. Stem, brachioles and cover plates unknown.

REMARKS. This Western Australian species is assigned to *Hyperoblastus* on its thecal shape, concealed lancet, radials covering main body of the deltoids, 5 spiracles and deltoid septum at depth within spiracles but not at surface. The phylogeny of the family has been discussed by Breimer & Dop (1975). Horowitz et al. (1986) and Waters & Horowitz (1993) and the occurrence and morphology of the new species do not conflict with their conclusions. The family is known from Europe, North America and China and its occurrence in the Frasnian of WA is in accord with European affinities of other elements of the fauna (Teichert, 1949). Breimer & Macurda (1972: 290) remarked on the paucity of blastoids in the Frasnian and Famennian worldwide; they acknowledged only a few specimens of *Hyperoblastus* from the Frasnian of the United States so the occurrence in the latest Frasnian of Western Australia suggests the

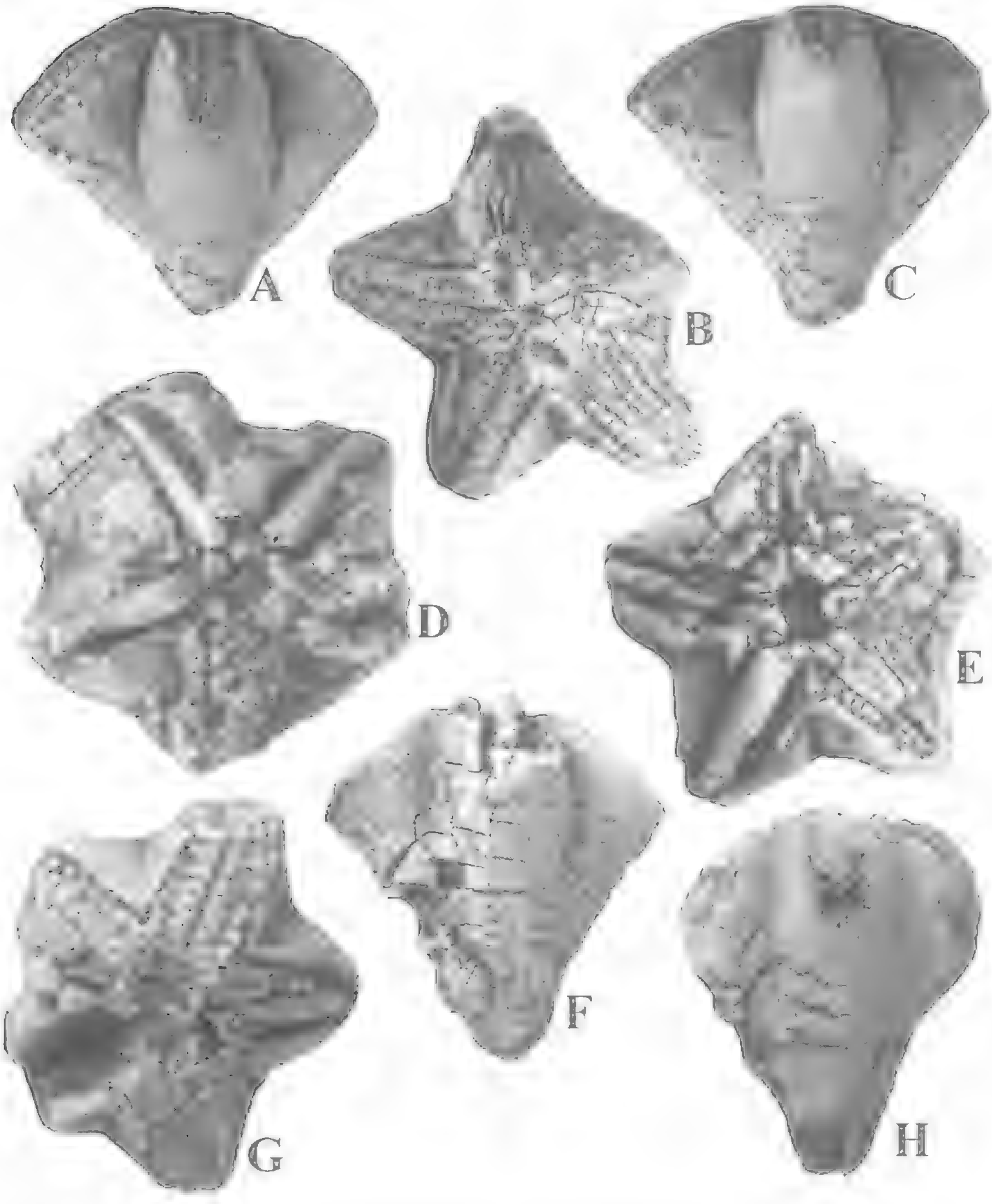



FIG. 3. *Hyperoblastus buglensis* sp. nov. all from QML1031. A-C, QMF36163. A, C, lateral oblique and lateral views, ×4. B, oral view, ×5. D, oral view of QMF36164, ×7. E,F, oral and lateral views of QMF36165, ×9 and ×5, respectively. G, H, oral and lateral views of QMF36166, ×7 and ×6, respectively.

lineage continued, but evidence of any other blastoid lineages is still lacking for this interval. Lane et al. (1997) erected *Sinopetaloblastus* from the Famennian of NW China and assigned it to the Hyperoblastidae but it is quite different, in gross shape, ambulacral structure and anal plating, from the new Australian form. Waters (1988) remarked that most blastoid genera were

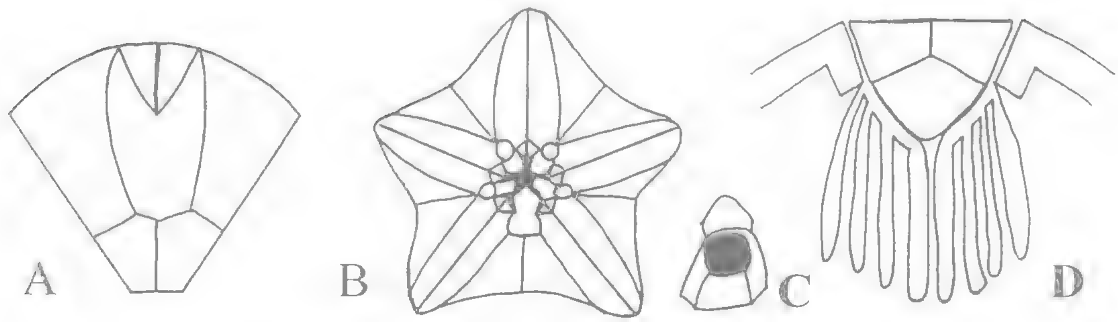



FIG. 4. *Hyperoblastus buglensis* sp. nov. A, lateral outline showing convex vault and straight sides. B, distal view showing spiracles, raised diamond-shaped adoral ends of lancets, and ambulacral tracts. C, analdeltoid arrangement with super-, sub- and hypodeltoid (composite from Fig. 2B showing hypodeltoid, Fig. 1D showing superdeltoid and Fig. 2F showing subdeltoid; each specimen at different level of weathering to expose different elements). D, cross section of an ambulacral tract to show arrangement of deltoids, lancet and hydrospires.

restricted to one or a few localities and very short time ranges; although *Hyperoblastus* has wide geographic and stratigraphic ranges the new species is known from only one locality and horizon.

Among known *Hyperoblastus*, only *H. eifelensis* (Roemer,1852) and *H. lusitanicus* (Etheridge & Carpenter, 1882) have the conical pelvis and low vault characteristic of the new species. The former is distinguished by the much greater number of hydrospire folds in each ambulacrum (Fay, 1961, text-fig. 84) and the latter is distinguished by its much smaller pelvic angle, smaller outer side plates and different sectional shape of the lancet (Fay, 1961, text-figs 90-93).

Subclass CAMERATA
Order MONOBATHRIDA
Suborder COMPSOCRININA
Superfamily HEXACRINITOIDEA Wachsmuth & Springer, 1885
Family HEXACRINITIDAE Wachsmuth & Springer, 1885

### **Hexacrinites** Austin & Austin, 1843

TYPE SPECIES. *Platycrinus interscapularis* Phillips, 1841 from the Devonian of England; by original designation.

### **Hexacrinites brownlawi** sp. nov.
(Figs 5,6)

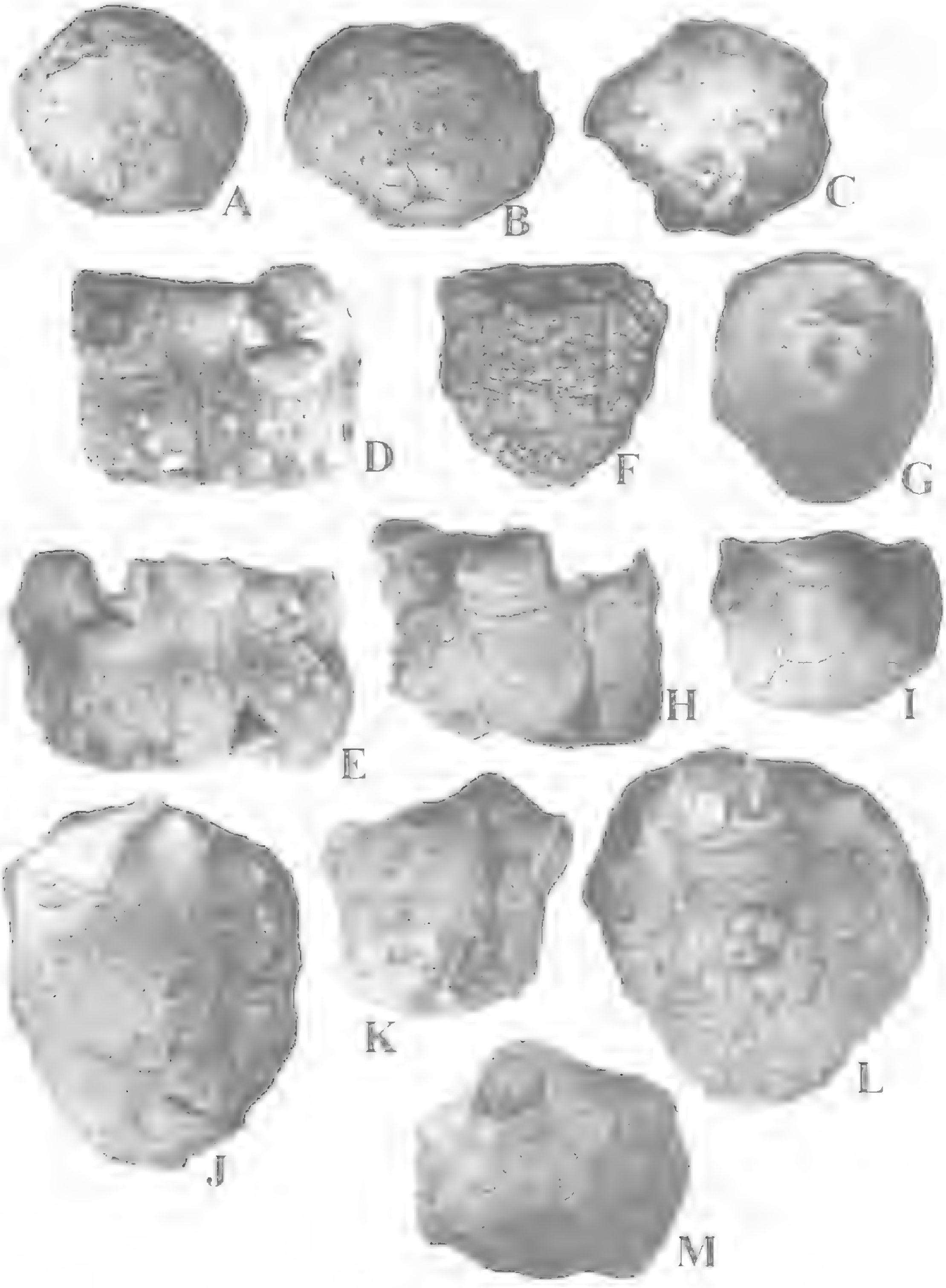
ETYMOLOGY. For Scott Brownlaw who collected some of the material.

MATERIAL. HOLOTYPE: GSWA115324. PARATYPES: QMF36169-36179, 40356. All from QML1031, on E side of Bugle Gap S of Wagon Pass.

DIAGNOSIS. Ornament of a few coarse tubercles with concave tips on most of theca, with distinct change to finely granulose ornament distally from just proximal to radial facet. Second primibrach axillary.

DESCRIPTION. Cup subcylindrical with widely flaring conical base, up to 28mm long and 22mm in diameter. Basal circlet hexagonal, of 3 equal plates; stem attachment facet moderately large, up to 6mm in diameter, with fine narrow marginal crenularium. Basals to radials suture usually wavy. Radials large, with convex proximal margin, with short upper lateral projections beside wide pene-plenary radial facets. First primibrach tapering laterally, narrower distally, with crenellate articulation facets proximally and distally. Second primibrach axillary, subtriangular and of variable width in lateral view, also with crenellate articulating facets. First secundibrachs of uniform length, thick, with wide deep ambulacral groove just beginning to divide. Rest of arms unknown. Primanal of similar size to radial,

FIG. 5. *Hexacrinites brownlawi* sp. nov. all from QML1031. A-C, oblique basal views of QMF36169, ×4, QMF36170, ×2, and QMF36171, ×2, respectively. D,E, 2 interadial lateral views of QMF36172, ×3. F, lateral view of weathered theca QMF36173, ×2. G, basal view of QMF36174, ×3. H, I, lateral views of incomplete thecae QMF36175 and QMF36176, ×2. J-L, QMF36177, ×2. J, C-D interradial view showing anal tube on right. K, oral view with anal tube at 6 o'clock. L, lateral view showing low axillary 2nd primibrach. M, distal view of theca QMF36178, ×2.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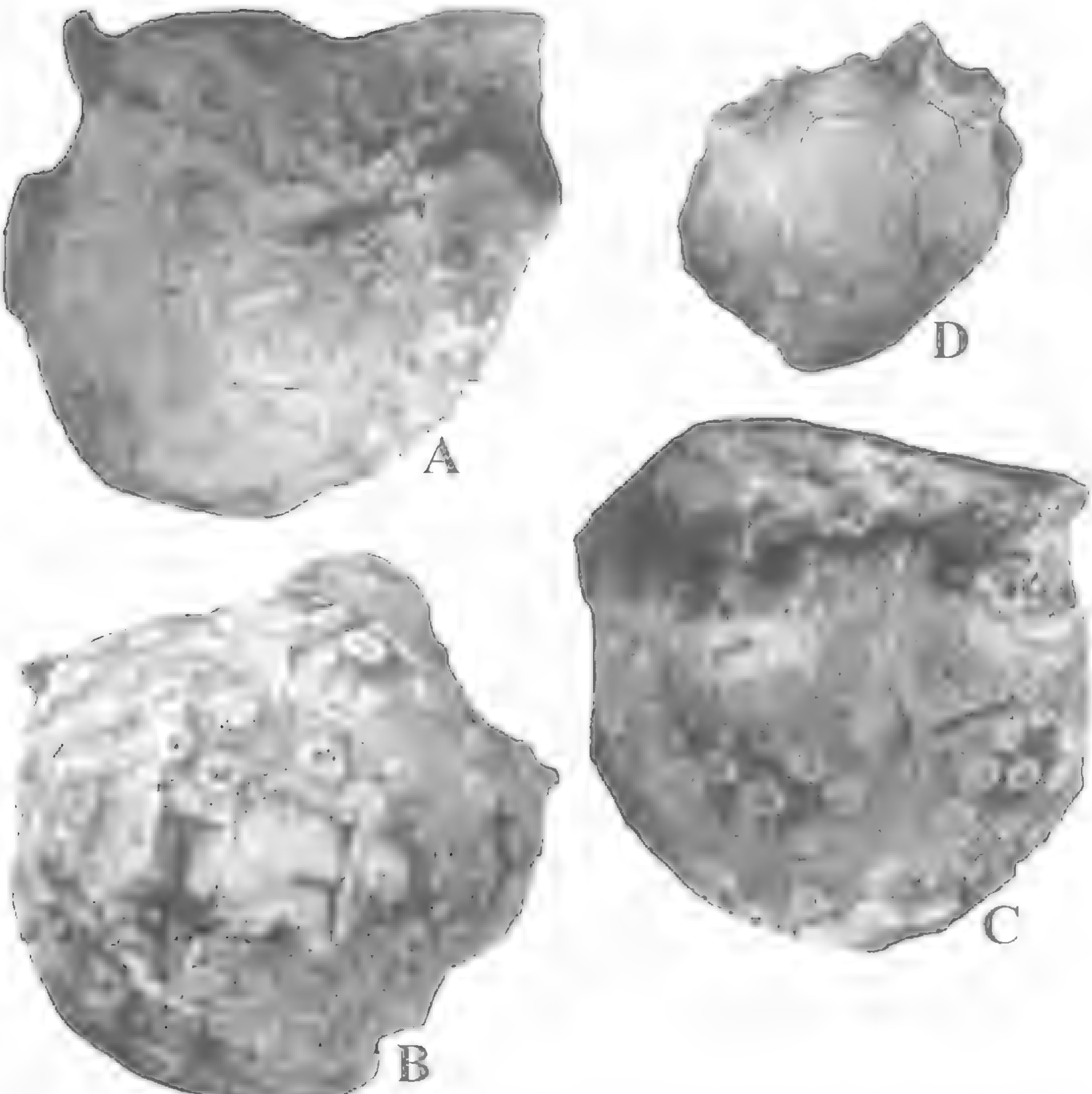



FIG. 6. *Hexacrinites brownlawi* sp. nov. all from QML1031. A-C, A ray, basal and C ray views respectively, of holotype GSWA115324, ×4. D, posterior view of QMF40356, ×2.

supporting 1 large tegminal plate distally. Anal opening on small spire rising from theca distal to 1st row of tegminal plates distal to primanal. Interprimibrachs 1 per interradius, large, supporting 1 or 2 smaller tegminal plates. Tegmen convex, inflated well distal to arm bases, longest anteriorly, sloping to posterior; tegminal plates of uniform size, polygonal, with central peak. Ornament on basals and radials proximal to arm bases, of few irregularly distributed large tubercles; tubercles with concave tips, usually more concentrated just proximal to radial facet, in one specimen (Fig. 5G) forming circlet around stem facet on slightly longer thecal base; distal to arm bases ornament changes sharply, becoming finely granulose.

REMARKS. Thecal shape resembles a number of other species of the genus including *H. spinosus* Muller, 1856 which occurs in the Middle Devonian of Queensland (Jell et al., 1988) but the inflated tegmen and ornament are distinctive.

### **Wacrinus** gen. nov.

TYPE SPECIES. *Wacrinus caseyensis* sp. nov.

ETYMOLOGY. For Western Australia.

DIAGNOSIS. First primibrach axillary. Fixed arms not forming protruberant brachial lobes but first free arm plates directed outward. Anal opening through tegmen in C ambulacral series of small plates; no anal tube developed. Tegmen plating usually strongly differentiated, with a single large interambulacral in each interray except CD where a number of smaller plates are present, with many ambulacral plates of varying sizes, with 5 orals at intersection of ambulacral tracts.

REMARKS. *Wacrinus* could be related to *Arthroacantha* Williams, 1883 from the Devonian of Europe and North America by its slender stem, ornament, single large interprimibrach and subtle ray ridges but that genus has 2 primibrachs per ray. *Cerasmocrinus* Strimple & Levorson, 1973 (type *Hexacrinus springeri* Thomas, 1924) from the Upper Devonian of Iowa was excluded from the Hexacrinitidae (and placed in the Desmidocrinidae) because its interprimibrachs penetrate the interradial area of the theca. However, its interprimibrachs bear exactly the same relationship to the tegmen, arms and radials as do those of *Hexacrinites interscapularis* (Ubaghs, 1978, fig. 279.1b,c) and *Wacrinus*; the only differences are in the extent to which the arms are fixed in the cup and relative size of radials and primibrachs. We suggest *Cerasmocrinus* should be returned to the Hexacrinitidae and is allied to *Wacrinus*.

Gary Lane (pers. comm. 1998) has drawn our attention to *Adelocrinus* Phillips, 1841 from the Famennian of SW England which he is currently revising and which he considers a valid genus related to *Arthroacantha* but separated from it by having only 1 primibrach (like *Wacrinus*). In so far as both *Adelocrinus* and *Arthroacantha* have articulating spines on the cup and this feature (presence or absence of spines) is not observable on the tuberculate *W. millardensis* its assignment to one of those genera is not possible. However, the current review of *Adelocrinus* and/or better material of *W. millardensis* would provide better understanding of the relationships of the genera. The 2 new species described below could be separated generically by allying *W. millardensis* with the tuberculate *Adelocrinus* as opposed to the smooth *W. caseyensis*. We take note of the variety of ornament on different species of *Hexacrinites* from tuberculate to ridged to smooth in assigning the 2 species to the new genus.

### **Wacrinus caseyensis** sp. nov.
(Figs 7-11)

ETYMOLOGY. For Casey Falls adjacent to the collecting site; Casey Falls are named for John Casey who was involved in mapping the area during the 1950's.

MATERIAL. HOLOTYPE: NMVP100280. PARATYPES: NMVP100272-100279, 100281-100300, QMF36180, GSWA19390-19393, WAM91.719, 91.722, 91.723 all from NMVPL1931, above Casey Falls; further specimens, mostly less well-preserved from the type locality are held in the Museum of Victoria, Queensland Museum, Geological Survey of Western Australia and the Western Australian Museum.

DIAGNOSIS. As for genus.

DESCRIPTION. Cup subspherical, 10-30+ mm long; plates smooth, without median ray ridges, thick. Basals 3, equal, pentagonal, forming hexagonal circlet, with intervening sutures in B and E rays and in CD interray, with low indistinct circular ridge centrally surrounding depressed (first columnal fills depression) crenulate stem facet. Radials largest plates of cup, heptagonal, A, B and E radials symmetrical, but C and D radials slightly asymmetrical in that suture with 1st interprimibrach is noticeably longer than that with anal plate distal to primanal. First primibrach axillary, with 5 straight sides (angles between them suggest hexagonal shape), distal margin with 2 broad shallow scallops for secundibrachs; 1st secundibrachs fixed in cup; 2nd secundibrach unknown but probably free; intersecundibrachs absent; facet on axillary primibrach with sharp but low median ridge, with minutely crenulate outer margin, with pustulose to minutely ridged surface adorally in transversely symmetrical pattern, with distal part smooth except for 2 tiny axial canal openings. First interprimibrach large, hexagonal, with lateral margins converging distally, at level of axillary primibrach, supporting 2 hexagonal interprimibrachs in second level; 2nd row interprimibrachs with sutural margins to axillary primibrach and to 1st ambulacral plates of tegmen, supporting a single large interambulacral in most cases but in a few rare cases (Fig. 9I) supporting 2 interambulacrals and in 2 cases (Figs 7G, 9B) large interambulacral of AB and BC interray resting directly on 1st interprimibrach and separating 2 second row interprimibrachs. CD interray with large hexagonal primanal in radial series but not as large as radials; 2 hexagonal plates in 2nd row resting on primanal and with distally converging lateral margins; 3rd row usually with 3 smaller plates

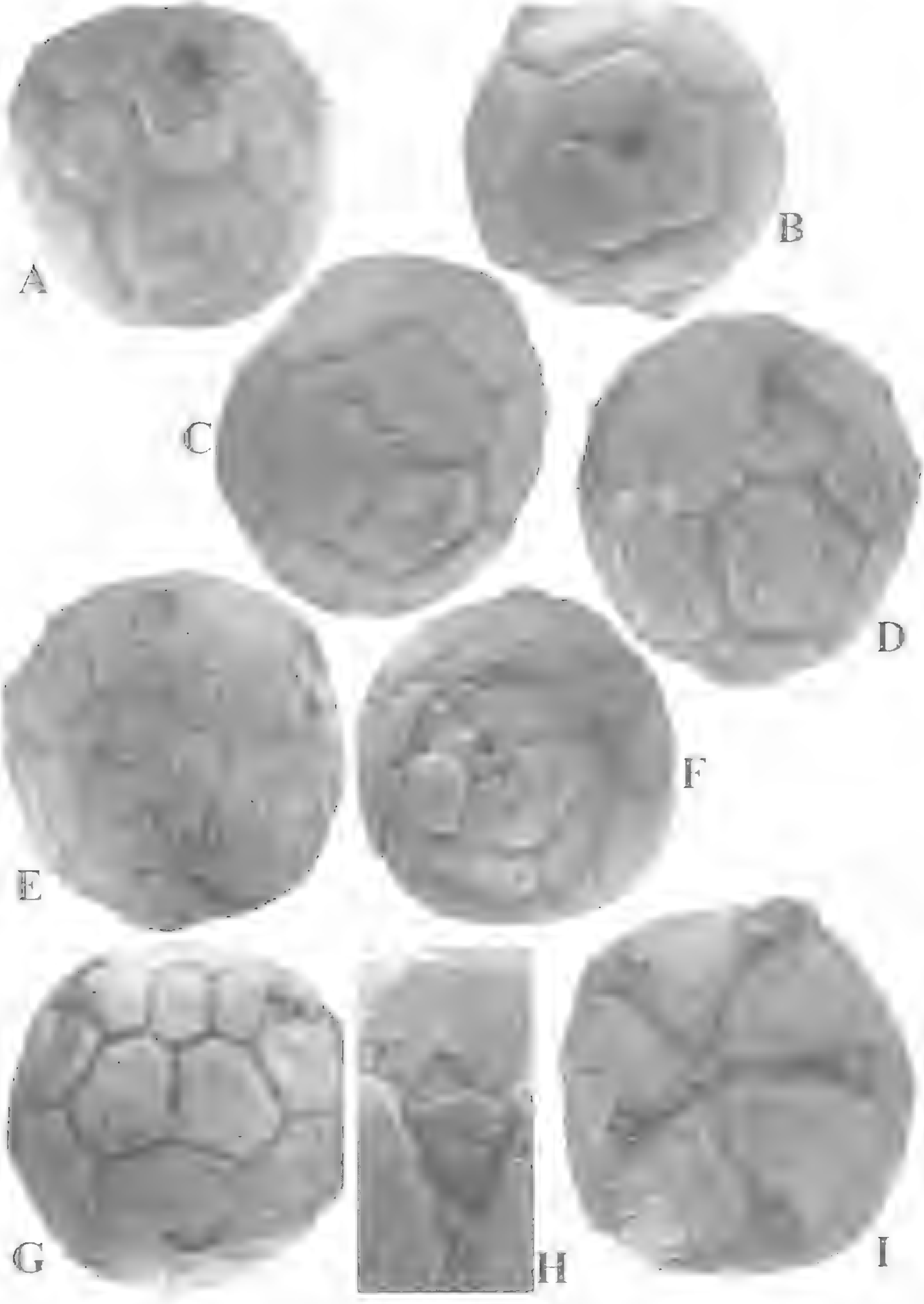



FIG. 7. *Wacrinus caseyensis* gen. et sp. nov. all from NMVPL1931. A,B, A ray and basal views of NMVP100278, ×4.5. C-E, basal, C radial and A radial views of NMVP100279, ×3. F, G, I, basal, C-D interray and oral views of holotype NMVP100280, ×2. H, radial facet of NMVP100281, ×4.5.

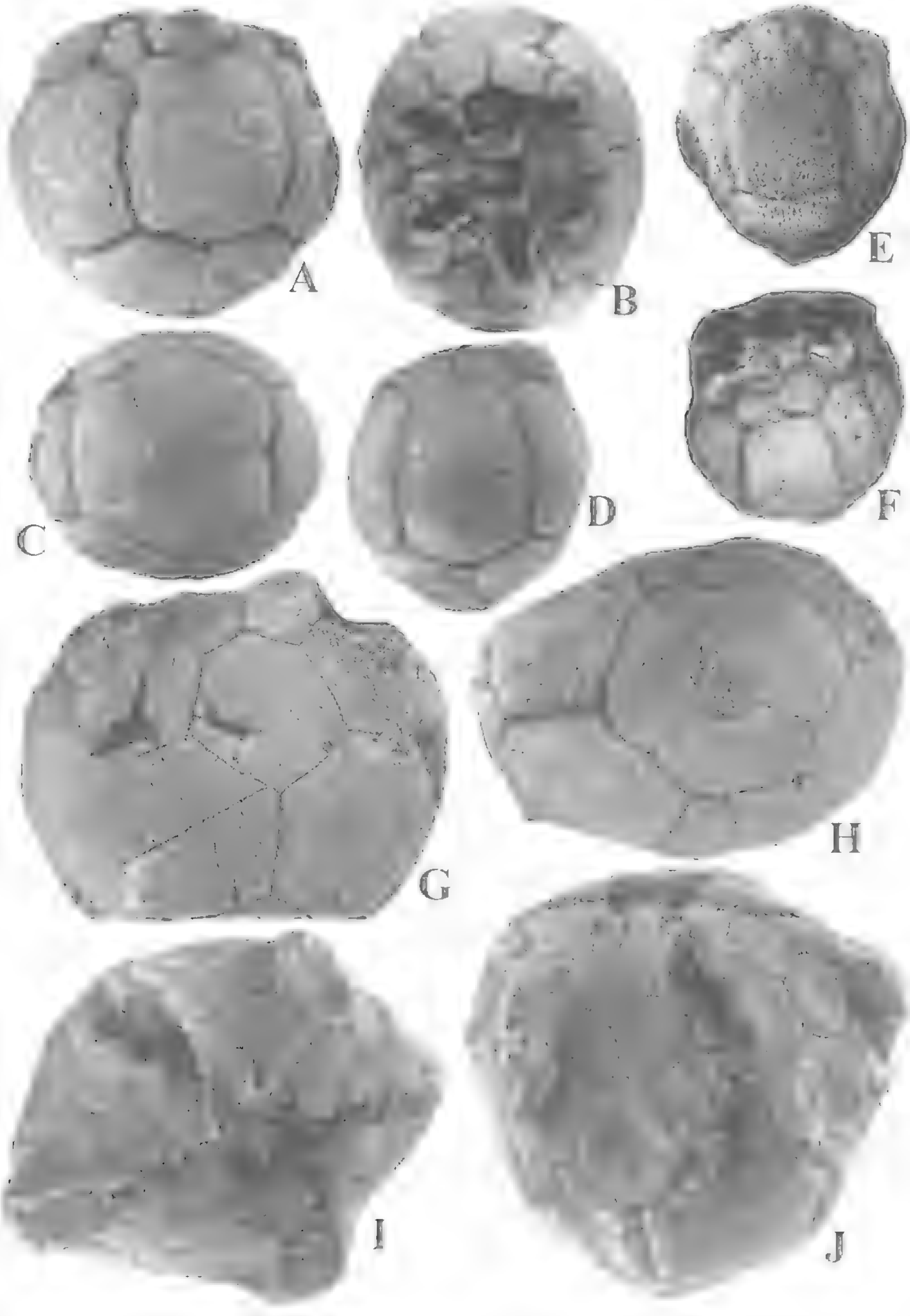



FIG. 8. *Wacrinus caseyensis* gen. et sp. nov. all from NMVPL1931. A-D, B radial, distal, proximal and C-D interray views of NMVP100282, ×5. E,F, A radial and C-D interradial views of WAM91.719, ×2.5. G,H, B ray and proximal views of NMVP100283, ×3. I,J, distal and E ray views of NMVP100284, ×4.

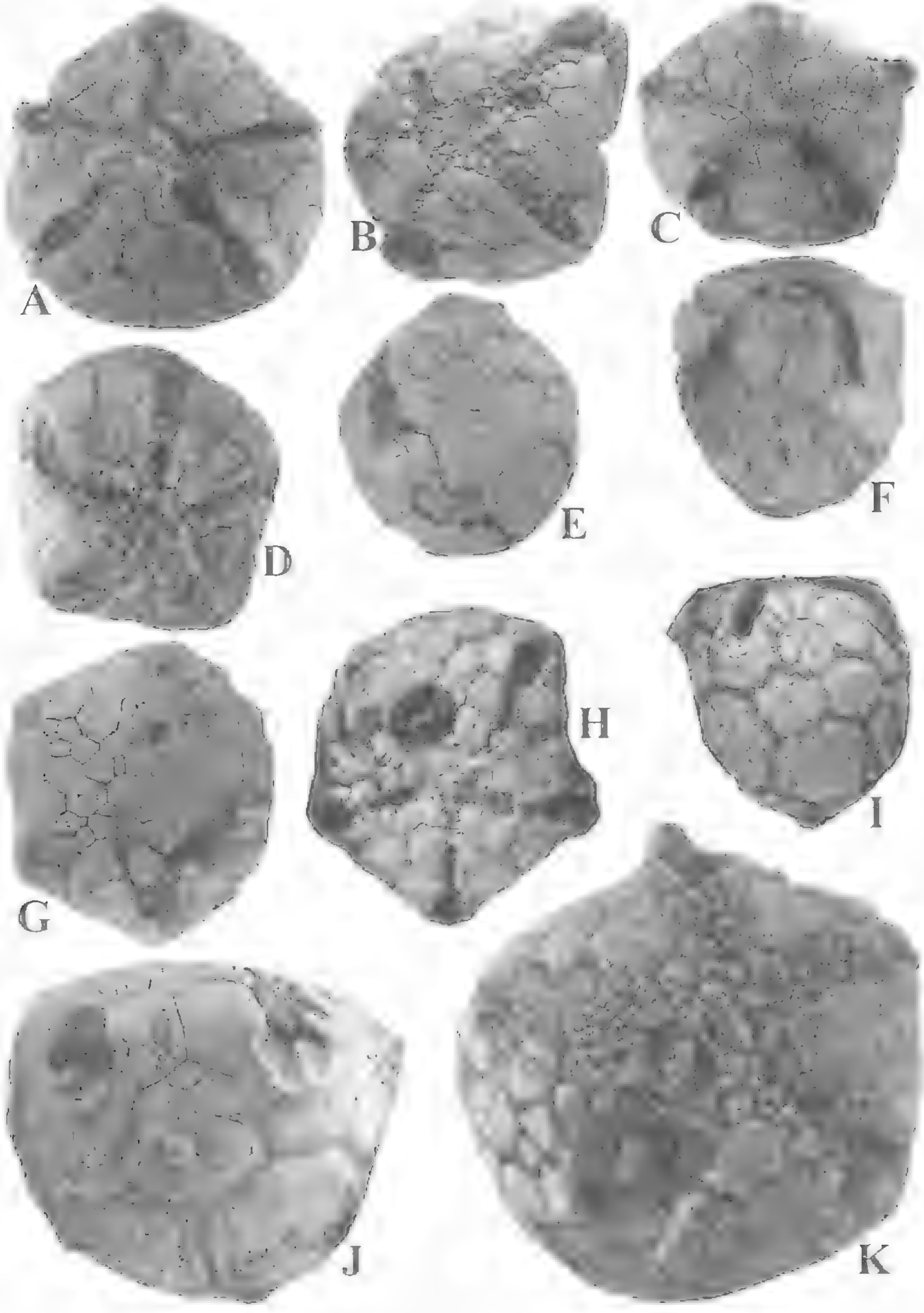



FIG. 9. *Wacrinus caseyensis* gen. et sp. nov. all from NMVPL1931. A-C, distal views of thecae. A, NMVP100272, ×1.8. B, NMVP100273, ×2.3. C, NMVP100274, ×1.8. D-F, distal and D-E and E-A interradial views of NMVP100275, ×1.8. G, J, distal and A-B interradial views of NMVP100276, ×1.8 and ×2.7, respectively. H, I, distal and C-D interradial views of QMF36180, ×1.8. K, distal view of NMVP100277, ×2.7.

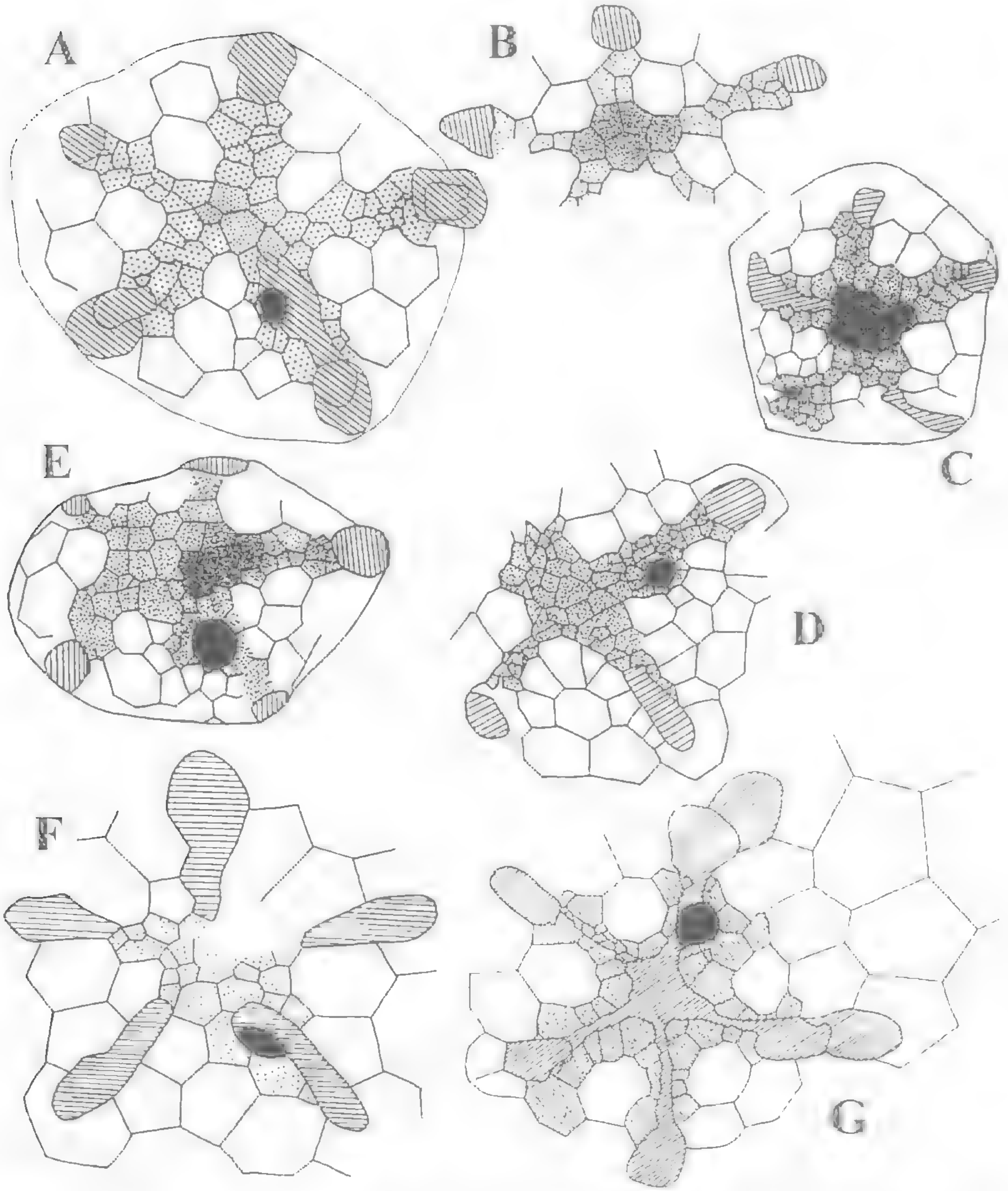
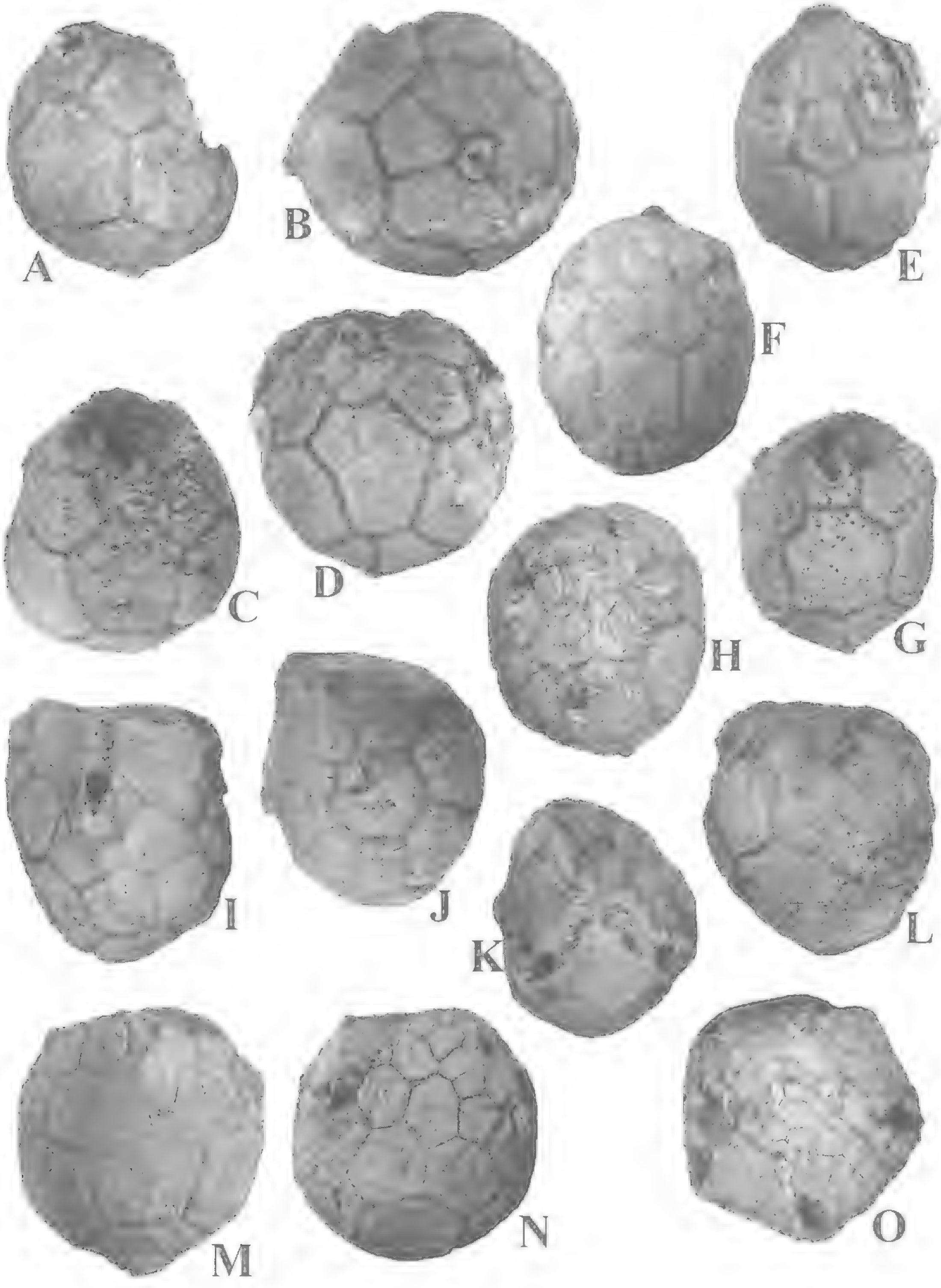



FIG. 10. *Wacrinus caseyensis* gen. et sp. nov. Camera lucida sketches of tegmens. Black = anal opening; lined = nonpreservation (as in arm bases and ambulacral tracts); light stiple = ambulacral plates (apparently thinner than interambulacrals because they weather more easily); heavy stiple = orals (5). A, NMVP100274 (Fig. 9C). B, NMVP100285. C, NMVP100275, (Fig. 9D). D, NMVP100273 (Fig. 9B). E, NMVP100286. F, NMVP100272 (Fig. 9A). G, NMVP100280 (Fig. 7I).

distally supporting 2 then 1 interambulacrals of variable size. Tegmen short, of many plates, plates well differentiated into ambulacrals and interambulacrals, ambulacrals usually small, forming 2 parallel series from each arm base to oral pole with considerable variation in size and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intercalation of small accessory plates, usually with 5 central interradial orals, with AB and EA orals in contact with the large interambulacral but BC and DE orals separated from interambulacrals by ambulacral plates; interambulacrals normally 1 (but sometimes 2 or 3) large plate in each interray except CD, several in CD interray of variable size and arrangement and also variable adjacent to anal opening; anal opening through tegmen without anal tube, situated in ambulacral plates of C ray halfway between arm base and oral pole, surrounded by tiny plates on all sides (generally weathering quickly so that details are rarely available). Stem of short columnals, with narrow areola and well-developed narrow marginal crenularium; diameter of stem apparently increasing distally.

*Morphogeny.* A well-preserved cup 10mm long indicates changes which accompanied growth to the average sized individuals (about 20mm long) and to the rare large individuals up to more than 30mm long. The major feature of growth is that the size of plates distal to the radial circlet which were tiny in the small individual increased in size relative to the basal and radial plates. Whereas in the small individual the 1st interbrachial is 1/6 length of the radial, in a theca only 13mm long this ratio had risen to 1/2 and in the largest theca to almost 5/6. Corresponding increases in relative sizes of brachial and tegminal plates are also apparent. Most of the tegminal plates have weathered off but the remnants of large interradial (presumably the large interambulacral) plates suggest that the ambulacral series was well-differentiated in the smallest individual as they are in the 13mm theca. It appears that at 10-20mm cup length, basals and radials grew at only 1/2 the rate of more distal plates.

Brower (1967) noted a similar change in relative growth rates in acrocrinitids; principally the radial plates which grew rapidly in earliest growth gradually assume a slower growth rate as more distal cup plates experience increased growth rates.

REMARKS. The thecae have weathered out of dark red silty beds that approach a coquina at some levels; they are scattered over the surface and are weathering continuously so perfect specimens are almost unknown. In most cases the first plates to weather are the small ambulacrals giving the tegmen the very obvious 5-rayed appearance.

The large collection of some 100 thecae gives a good understanding of intraspecific variation. Almost all this variation appears to be confined to the tegminal plates; certainly there is no variation in the basal or radial circlets. As already mentioned in the description, the number and arrangement of second row interbrachials and interambulacrals have a few variations but in <10 specimens whereas the variation in size, shape and arrangement of both ambulacral and CD interambulacral plates is much more widespread.

Several aberrant individuals are known; one has 4 basals (Fig. 11B), 7 plates in the radial circlet (Fig. 11B), a peculiarly shaped 7-sided E radial (Fig. 11D) and asymmetrical tegmen (Fig. 11A). It appears the anterior interprimibrach is forced into the radial circlet, contacting the basal circlet and demanding an extra side to that circlet; the strange E radial appears to be a fusion of 2 plates, the radial and a second row interbrachial of the anterior interradius which is moved proximally with the 1st interprimibrach. It is not clear how this aberrant growth came about as injury is not evident and there is no evidence of disease or parasitism. Another specimen has only 3 ambulacral tracts on the tegmen and thus only 3 arms (Fig. 11K); in the radial circlet between A and D radials it has 2 plates that do not lead into normal arm bearing rays (Fig. 11J); it has 3 anal plates resting on the primanal (Fig. 11L) as opposed to the normal 2. Again the cause of this aberrancy is unclear although regrowth after a predatory removal of 2 arms at an early growth stage might be expected.

### **Wacrinus millardensis** sp. nov.
(Figs 12,13)

ETYMOLOGY. For Millard Creek adjacent to the type locality.

MATERIAL. HOLOTYPE: QMF36190. PARATYPES: QMF36191-36193, WAM91.715, 91.716, 91.718, 91.720, 91.721 all from QML1030 above Casey Falls.

DIAGNOSIS. Cup small (up to 18mm long), basals and radials with large irregularly spaced tubercles and median ray ridges; 1st primibrach

FIG. 11. *Wacrinus caseyensis* gen. et sp. nov., all from NMVPL1931. A-D, lateral B ray, proximal, lateral D ray and lateral E ray views of aberrant cup GSWA19390, ×1.5. E, F, lateral D-E interray and posterior views of WAM91.722, ×2. G,H, lateral B ray and posterior views of GSWA19391, ×1.5. I-L, lateral B ray, lateral D ray, distal and posterior views of aberrant, 3-armed, cup GSWA19392, ×1.5. M,N, anterior and posterior views of WAM91.723, ×2. O, distal view of GSWA19393, ×1.5

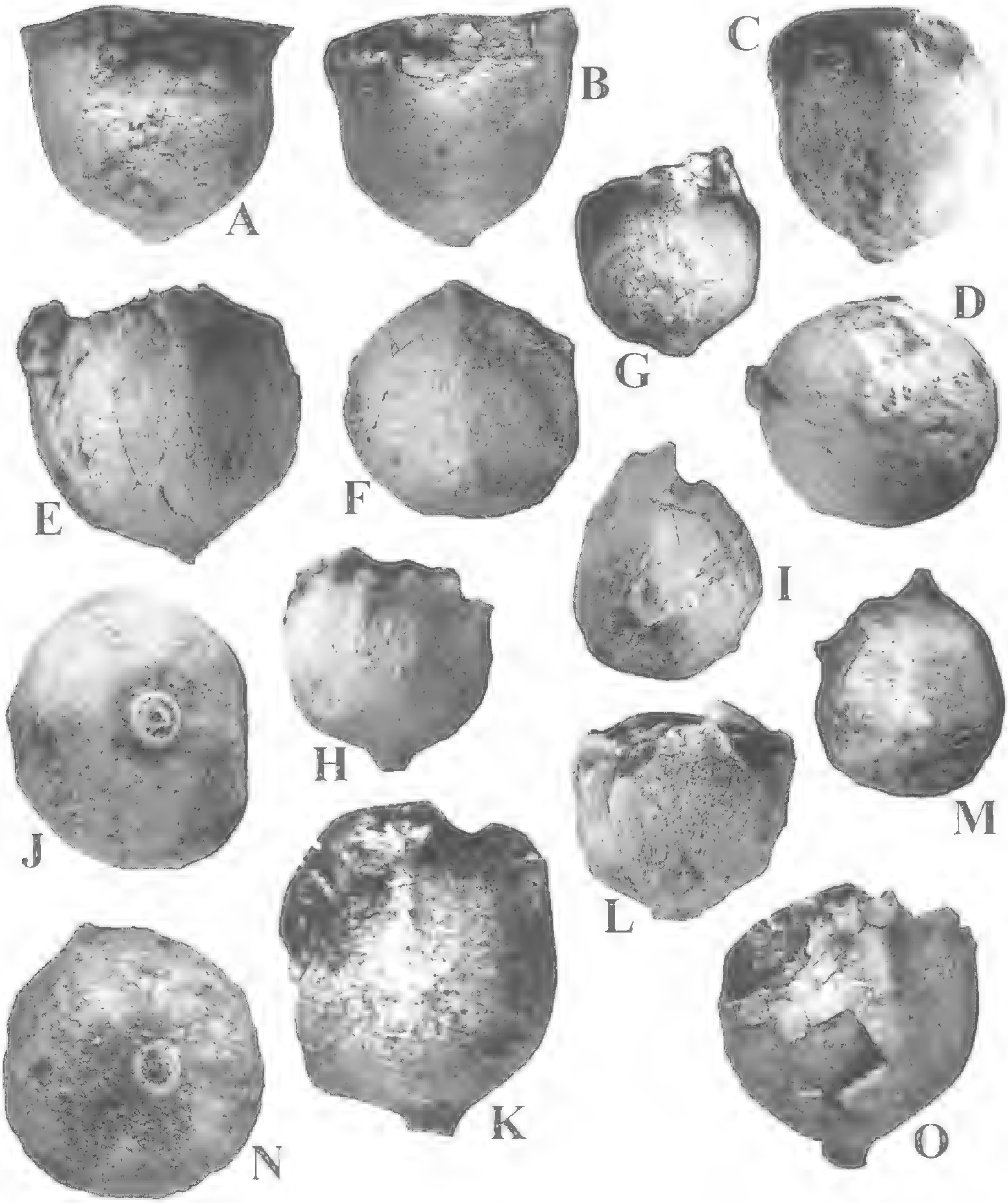


FIG. 12. *Wacrinus millardensis* gen. et sp. nov. A-D, C-D interradial, E-A interradial, A radial and basal views of holotype QMF36190, ×2. E-H, Lateral views of WAM91.721, WAM91.718, WAM91.715, WAM91.716, ×2. I, Basal view of WAM91.720, ×2. J, K, Basal and lateral views of QMF36191, ×2.5. L, M, Lateral and basal views of QMF36192, ×2.5. N, O, Basal and lateral views of QMF36193, ×2.

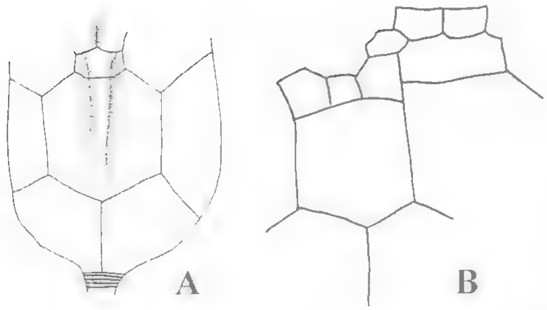



FIG. 13. *Wacrinus millardensis* gen. et sp. nov. Camera lucida sketches of plate arrangement. A, A ray view of cup showing shape of 1st primibrach and position of ray ridge (drawn from WAM91.721, Fig. 12E). B, posterior interray (C radial surmounted by axillary 1st primibrach and 2 secundibrachs on right) showing primanal supporting 3 plates distally (drawn from QMF36190, Fig. 12A).

transversely subrectangular, fixed in theca, axillary, with 2 distal curved sides (at interbrachial sutures) meeting in middle of ray in sharp point; 1st secundibrach fixed in cup; interprimibrachs large, 1 per interray, with smaller tegminal plates distally, extending just proximal to primibrachs with obtuse angle between distal margins of adjacent radials; stem round in section, with small diameter relative to theca.

DESCRIPTION. Cup high bowl-shaped, with elongate convex base. Narrow ray ridges most prominent on primibrachs and distal part of radials, extending to stem facet in some specimens. Hexagonal basal circlet of 3 equal plates, with sutures in B and E rays and C-D interray. Radials 5, large, convex, 6- (A, C and D radials) or 7-sided (B and E radials), with wide horizontal distal suture to primibrach; radial facet angustary. First primibrach subrectangular to pentagonal, axillary, with Y-shaped ray ridge dividing into the 2 arms, with curved distal margins at interbrachial sutures meeting in sharp point in ray axis. First secundibrach fixed in cup, with broad deep groove on distal side and fine central canal piercing the plate medially beneath the groove. Remainder of arms unknown. Primibrachs and 1st secundibrachs sutured to interbrachial plates. Primanal about same size as radials, supporting 3 plates distally (smaller central and equal laterals). Interbrachials 1 per interradius, large, abutting primibrach and 1st secundibrach, extending proximally between radials by distance equal to length of primibrach giving proximal margins a junction at about 120°. Tegmen unknown. Ornament on cup of coarse tubercles, becoming less obvious with growth, organised into colinear lines with margins in few specimens (most often removed by weathering). Stem slender, of very short columnals, with circular, flat attachment facet, pierced centrally by extremely fine axial canal.

REMARKS. This species does not reach the size of *W. caseyensis* and differs in having ray ridges, relatively small axillary primibrach with distal pointed tip and distinct cup shape (subcylindrical in distal part and slightly elongate base).

Suborder GLYPTOCRININA Moore, 1952
Superfamily MELOCRINITOIDEA d'Orbigny, 1852
Family MELOCRINITIDAE d'Orbigny, 1852

**Melocrinites** Goldfuss, 1831

TYPE SPECIES. *Melocrinites heiroglyphicus* Goldfuss, 1831 by subsequent designation of Roemer, 1855 from the Upper Devonian of western Europe.

**Melocrinites solidus** sp. nov.
(Figs 14-17)

ETYMOLOGY. Latin *solidus*, thick, entire.

MATERIAL. HOLOTYPE: WAM91.703. PARATYPES: QMF36194-36196, WAM91.701 all from QML1029, in Millard Creek just W of Casey Falls.

DIAGNOSIS. Radials making up large part of thecal length; 1st primibrach usually hexagonal, with 2 distal lateral margins narrow and distal central margin concave proximal to the arms, often axillary; 2nd primibrach very short, axillary; arms (2 per ray) fused into a solid trunk, with secundibrach 2 axillary (and giving off the first auxilliary arm (of Kesling, 1964)); more distal arms arising slightly irregularly but from about every 5th or 6th brachial; tegmen of few (c. 10-14) large plates; interprimibrachs few, 1st in contact with radial and 1st primibrach, 2nd row of 2 between arms butting up to tegmen plates. Plate arrangement irregular in some specimens. Ornament of vermiform ridges highly variable from barely evident to dense over whole plates.

DESCRIPTION. Cup of medium length (up to 30mm; mainly 20-25mm), from short (e.g. 20mm long and 20mm diameter) to long (e.g. 27mm long 19mm diameter) conical; surface of plates smooth to highly ornamented, varying between plates of 1 individual and between individuals; ornament of vermiform ridges and isolated tubercles, often reaching sutural margins in basals and radials but usually with a smooth marginal zone particularly on tegmen. Basal

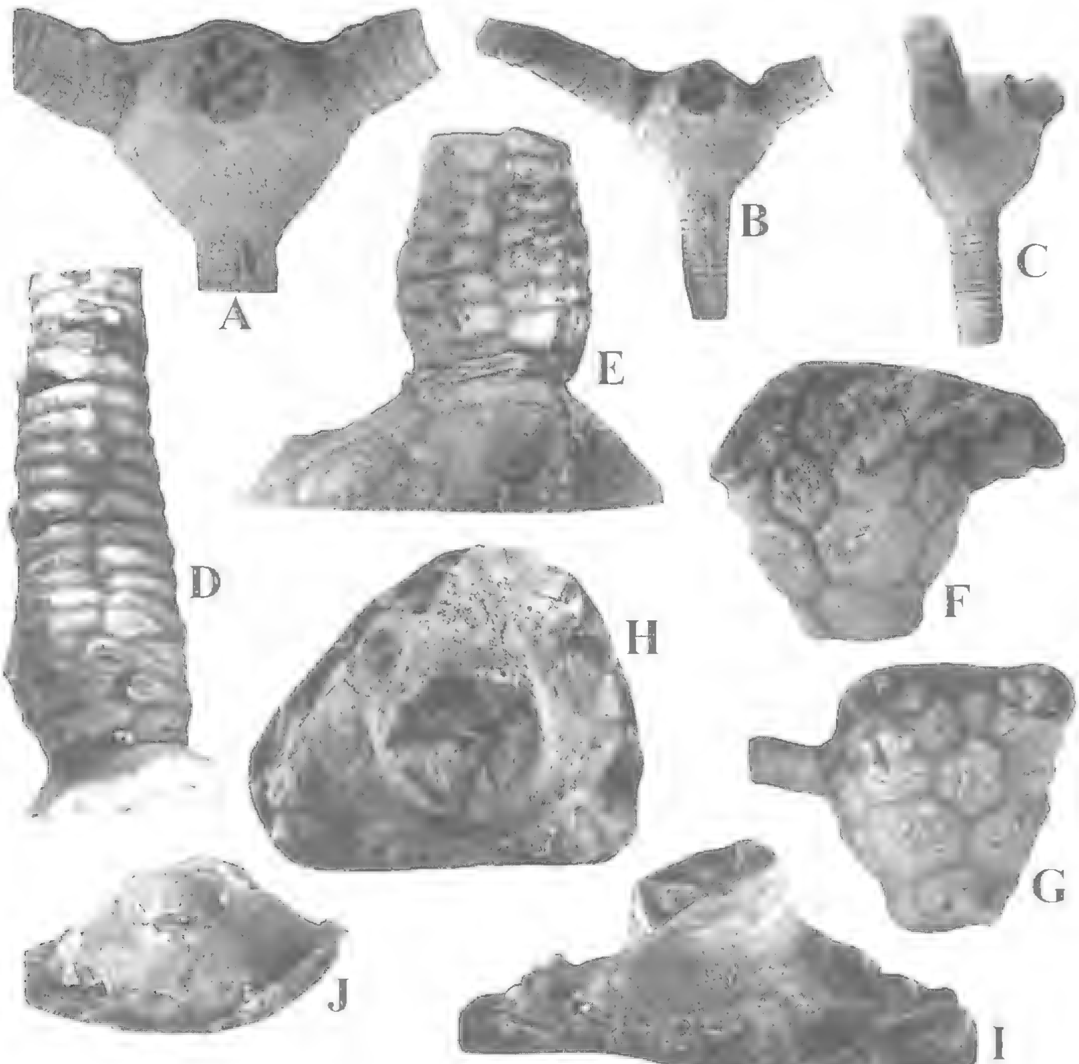


FIG. 14. *Melocrinites solidus* sp. nov. all from QML1029. A-E, QMF36196. A-C, lateral views, ×1.5, ×1 and ×1, respectively. D,E, arms viewed from underside, showing fused columns of the 2 arms, ×3. F,G, lateral views of juvenile WAM91.701, ×2. H,I, holdfast in plan and lateral views QMF36197, ×1. J, lateral view of holdfast QMF36198, ×1.

circlet of 4 plates, with interplate sutures positioned variably (B, C, D and A (QMF36195) or E (QMF36194) rays; basals pentagonal, up to 6mm long in lateral view, together forming circular stem facet proximally; stem facet flat, with irregular crenularium about 1/3 stem radius around margin, with medium sized axial canal, with slight indentations at sutures. Radials 5, contiguous, up to 10mm long and wide, 6-sided, or 7-, depending on position over 1 or 2 basals. First primibrach 6-sided, with horizontal suture against radial, with distal margin curved proximal to arm, with widest point distal to midlength. Second primibrach short, pentagonal, axillary, with short distal central peak, not present in every ray (Fig. 14A, B). Secundibrachs all short, suturally fused to those of other arm in same ray, with zigzag or straight junction between 2 arms in different places. Second secundibrach axillary, giving rise to short stumpy auxilliary arm. Distally every 5th, 6th or 7th brachial axillary, giving off stout arm vertically. Each ray trunk constricted at junction with theca, of greatest diameter at about 2nd or 3rd

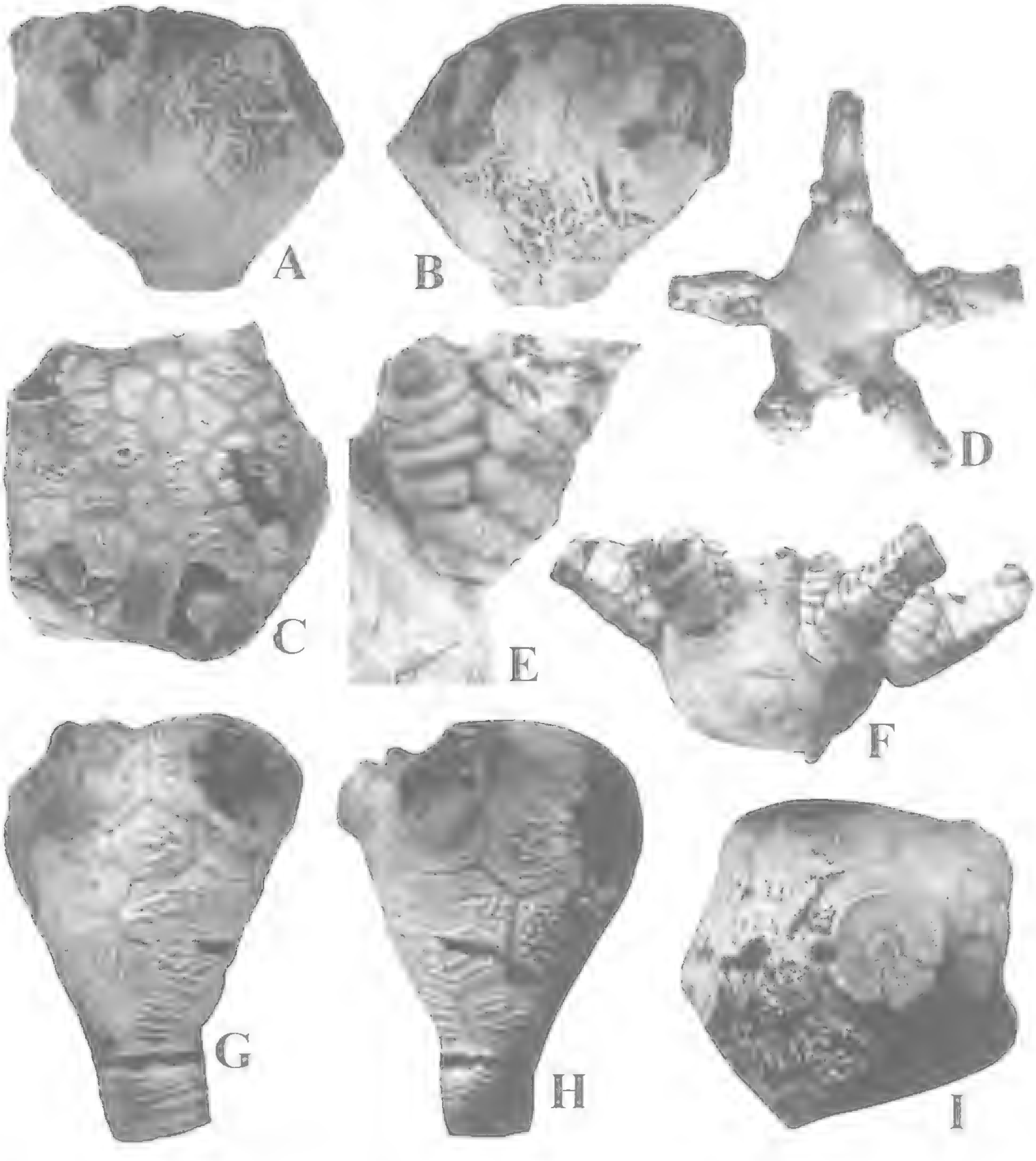



FIG. 15. *Melocrinites solidus* sp. nov. all from QML1029. A-C, Two lateral and tegminal views of QMF36194, ×2. D-F, Holotype WAM91.703. D, Tegminal view, ×1. E, lateral view of base of arm showing axillary second primibrach, ×3. F, Lateral view in C-D interray showing anal tube, ×1.5. G-I, Two lateral and a basal view of QMF36195, ×2.

secundibrach, with food groove completely sealed above by small convex irregular cover plates, pierced by large elliptical canal nearer to cover plates. Interbrachial facets covered with long anastomosing culmina and crenellae indicating immovable ligamentary junctions. Interprimibrachs few: 1st interprimibrach hexagonal, resting on radials, supporting 2 high

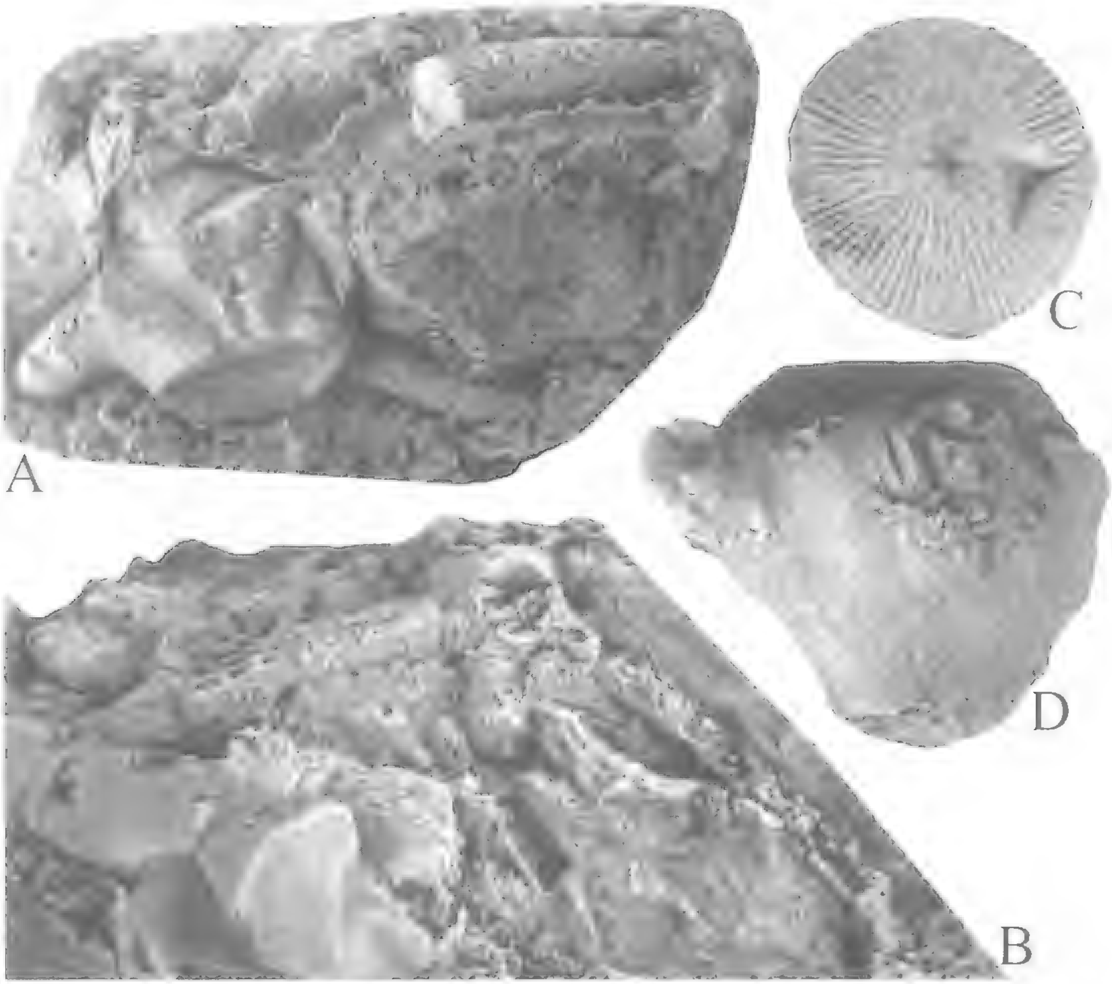


FIG. 16. *Melocrinites solidus* sp. nov. all from QML1029. A, proximal view of strongly rooted holdfast QMF36199, ×3. B, lateral view of strongly rooted holdfact QMF36200, ×2.5. C, end view of piece of stem showing extensive crenularium QMF36205, ×3. D, lateral E ray view of cup QMF36206, ×1.5.

plates in next row between arm bases; 2nd row reaching tegmen plates. Intersecundibrachs absent. C-D interray variable in available specimens; primanal supporting 2 or 3 plates distally; in WAM91.703 primanal apparently made up of 2 pentagonal plates with slight constriction at their junction. Stem circular in section, of large variable diameter up to 10mm; short columnals with row of pointed tubercles at midlength; with ligamentary articulation having wide marginal crenularium. Aureola wide on facet at base of cup but very narrow distally. Crenula dividing once or twice near midradius of facet.

REMARKS. This species is most closely allied to the Upper Devonian species of western Europe. The type species, *M. heiroglyphicus* Goldfuss, which occurs in the Frasnian of Germany, Belgium and England has similar plate ornament, cup shape and other general proportions. However, the new Australian species is distinguished by the shape of its first primibrach, the fewer plates in its tegmen and all secundibrachs being free of the cup. These features also distinguish the other Upper Devonian species of the Kuzbass (Dubatalova, 1964) and northern Canada (Springer, 1920). The new species is also distinguished from the 2 Middle Devonian species from eastern Australia (Jell et al., 1988) by its free secundibrachs and shape of its axillary primibrach. None of the known North American species have the combination of ornament, free secundibrachs,

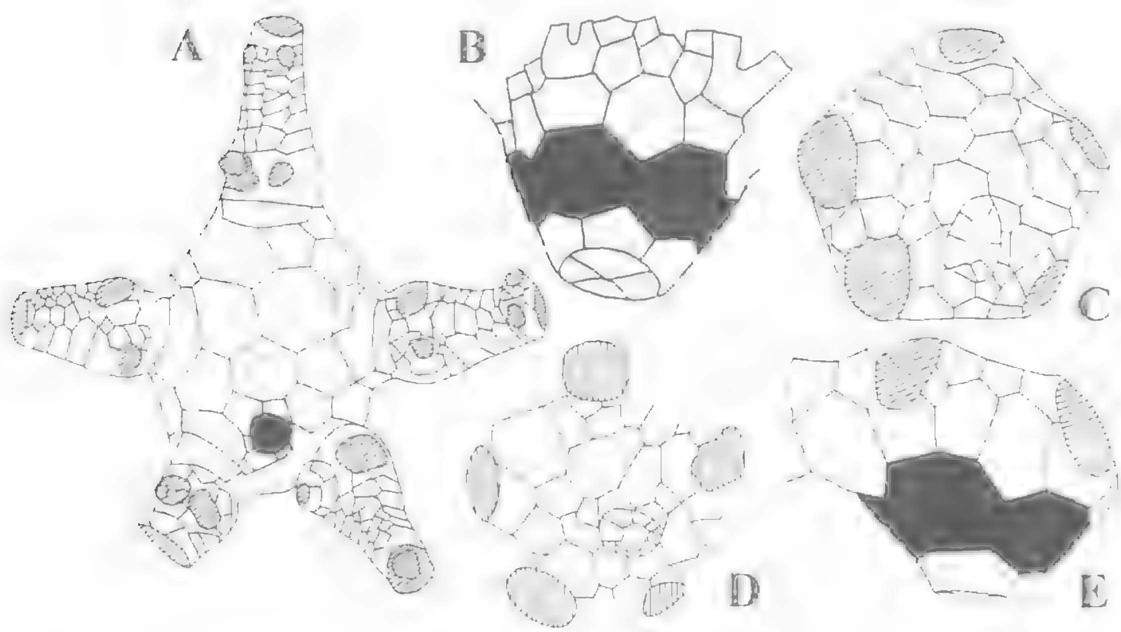



FIG. 17. *Melocrinites solidus* sp. nov. Camera lucida sketches. A, distal view of tegmen of WAM91.703 (Fig. 15D-F); solid black = anal tubercle, lined = fractured arm extremities and bases of ramules, in some areas (e.g. CD interray) sutures not evident. B, posterior oblique view of small cup showing 4 basals, primanal supporting 3 anals WAM91.701 (Fig. 14F, G), solid black = radials. C, distal view of tegmen of QMF36195 (Fig. 15G-I); lined = broken arm bases, oval ringed on inner side by small plates = anal tubercle. D,E, QMF36194 (Fig 15A-C); lined = broken arm bases, solid black = radials. D, distal view of tegmen with anal tubercle at lower centre. E, lateral view showing aberrant interray with 2 interprimibrachs in proximal row and normal interray to left.

few tegmen plates and 1st primibrach shape seen in the new Australian species. While the large number of existing specific names applied in this genus is an incentive to avoid creating more this species is quite distinctive and requires specific recognition.

Subclass DISPARIDA Moore & Laudon 1943
Superfamily PISOCRINOIDEA Angelin, 1878
Family PISOCRINIDAE Angelin, 1878

### **Jaekelicrinus** Yakovlev, 1949

TYPE SPECIES. *J. bashkiricus* Yakovlev, 1949 from the Frasnian of Bashkiria; by original designation.

REMARKS. Rozhnov (1981) reviewed the genus, described in detail the type and the only other species assigned, *J. yakovlevi* Rozhnov, 1981, and provided numerous plate diagrams for both species. He distinguished the genus from its ancestor *Calycanthocrinus* Follman, 1887 by the greater number of pararadials (12-23) and thicker calical plates.

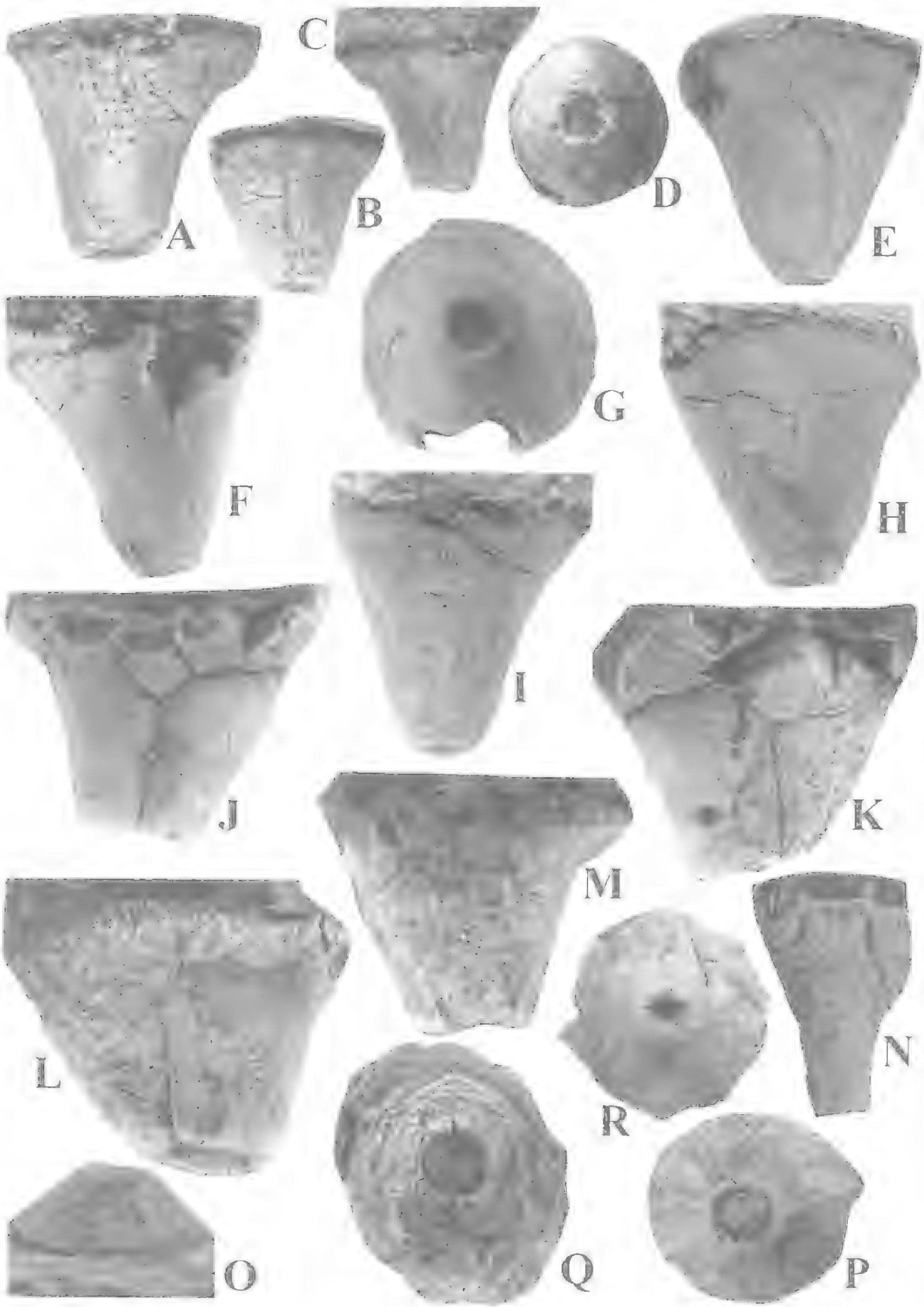
### **Jaekelicrinus murrayi** sp. nov.
(Figs 18-20)

ETYMOLOGY. For Dr Peter Murray, Northern Territory Museum who greatly facilitated collecting this material.

MATERIAL. Holotype: NMVP100308. Paratypes: NMVP100301-100304, 100308-100310 all from NMVPL1936, S of the Teichert Hills.

DIAGNOSIS. Basals 3, unequal, with largest basal having peaks at both distal corners and situated proximal to A radial, with some variation in course of suture between basals and radials; pararadials 12.

DESCRIPTION. Cup up to 12mm long, high conical or with slight lateral bulge in A ray producing suboval section, with marked increase in diameter at distal margin of radial circlet due to strong flaring of pararadial plates in some specimens. Base of cup with wide concave stem facet. Basals 3, unequal, forming short circlet, with relatively large circular concave stem facet pierced by small rimmed median canal; largest basal with peaks on both distal corners and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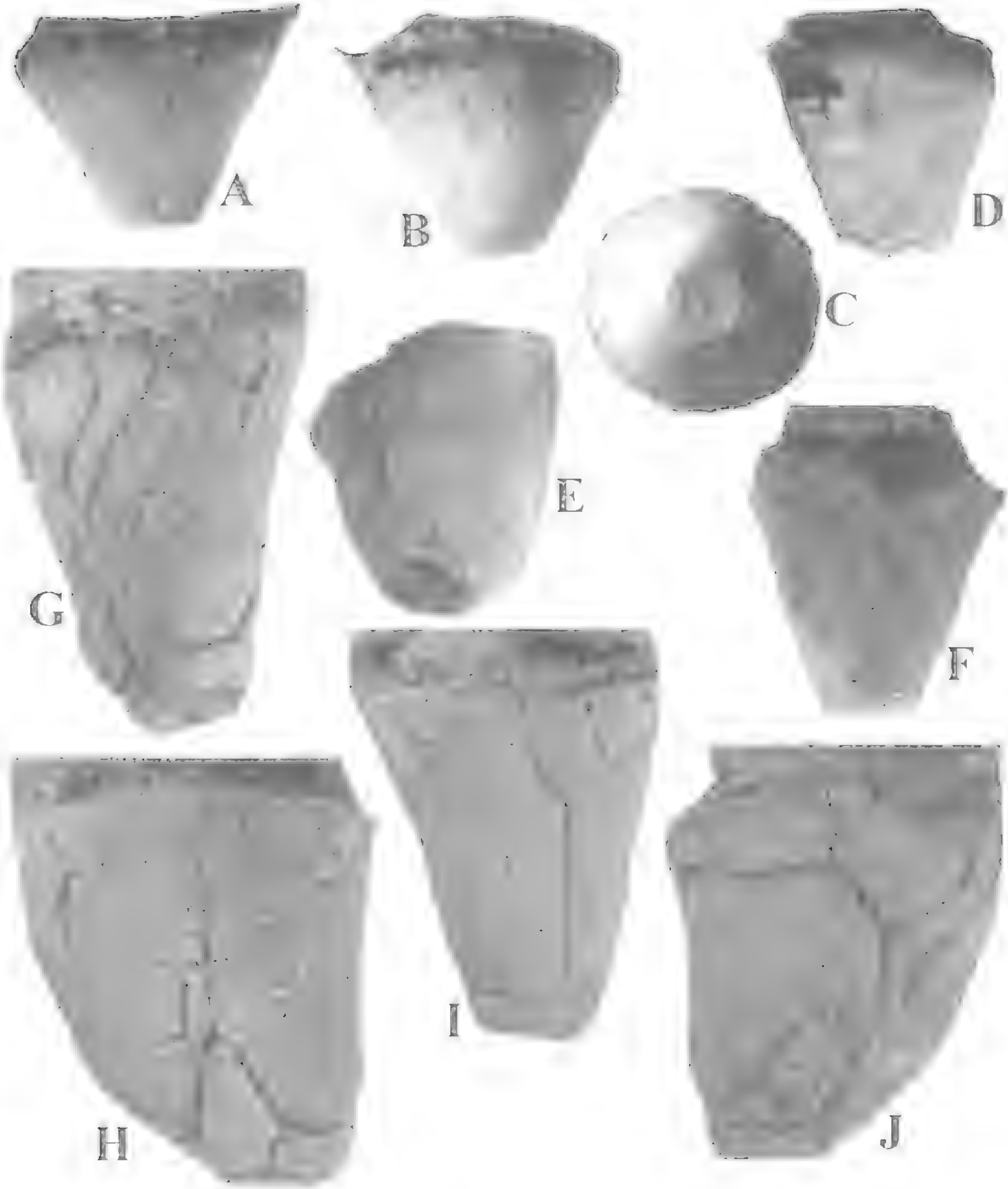


FIG. 19. *Jaekelicrinus murrayi* sp. nov. A-C from QML1029; D-J from NMVPL1936. A-C, lateral views except basal view C of QMF36201, ×5. D, lateral view of QMF36202, ×3. E, F, lateral views of NMVP100309, 100310, ×5. G-J, lateral views of holotype, NMVP100308, ×4.

FIG. 18. *Jaekelicrinus murrayi* sp. nov. A-M from NMVPL1936; N-R from QML1951. A-E, lateral views except D a proximal view of NMVP100301. A, C, E, ×4. B, x3. D, ×2.5. F-I, lateral views except G a proximal view of NMVP100302, ×6. J-M, lateral views of NMVP100303, ×5. N, lateral view of NMVP100304, ×4. O,P, lateral and plan views of holdfast NMVP100305, ×2. Q, R, plan views of holdfasts NMVP100306, 100307, ×2.

situated proximal to A radial, with sutures separating other basals situated proximal to B infraradial and D radial; 2nd largest basal with peak on only 1 distal corner, proximal to D radial, with suture to smallest basal proximal to B infraradial; smallest basal proximal to B infraradial. Radials of 2 distinctly different sizes; A and D very large, occupying nearly 2/3 of cup, variable in shape but usually widening distally then contracting markedly where pararadials intervene and expanding again just proximal to single radial facet; B, C and E radials small of highly variable size, often impossible to distinguish from pararadials, each with single radial facet; B infraradial nearly as large as A and D radials and occupying nearly 1/3 of cup, of variable shape; pararadials 12, of highly variable shape, size and arrangement, each with single radial facet, often very difficult to distinguish from smaller radial plates particularly E radial; radial facets occupying almost full width of plate but leaving very narrow vertical projections laterally at sutural margins, with characteristic vertical grooves within the plate just proximal to the facet in slightly weathered specimens.

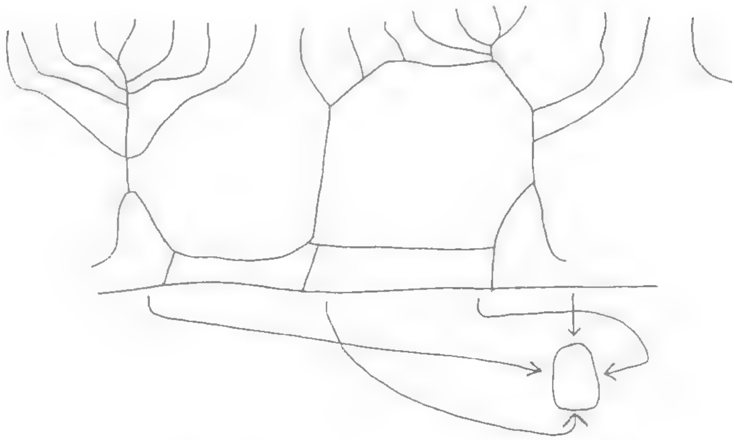

FIG. 20. *Jaekelicrinus murrayi* sp. nov. Camera lucida sketch with indication of which sides of cup are illustrated where; interplate suture at far right is same as that at far left; upper margins of radials and infraradials not shown; NMVP100308 (Fig. 19G-J).

REMARKS. This species is most closely related to the type species from which it may be distinguished by the 3 unequal basals, the E radial being so similar to the pararadials and the number of radial plates between A and D radials through E ray compared to single pararadial between A and B radials. It may be distinguished from *J. yakovlevi* Rozhnov, 1981 from the Frasnian of Bashkiria by the fewer paradials, the different situation of the various sized basals and the relatively undifferentiated E radial. *J. murrayi* must be considered a descendant of *J. bashkiricus* on a separate lineage from *J. yakovlevi*. The enormous amount of variation mentioned in the description of these few specimens is such that the possibility of *J. bashkiricus* and *J. murrayi* belonging to one species cannot be overlooked. However, the arrangement of plates rather than their shape and size is probably distinctive. Larger populations of both species will be necessary to be certain of this distinction. The highly variable nature of the cups available, also makes biometric studies useless until larger collections are available.

## **Playfordicrinus** gen. nov.

TYPE SPECIES. *Playfordicrinus kellyensis* sp. nov.

ETYMOLOGY. For Dr Phillip Playford for his contribution to understanding of the Devonian of the Canning Basin.

DIAGNOSIS. Cup subspherical, with widely spaced fine granular ornament. Basals 3, irregularly shaped, each asymmetrical with a distal projection at sutures between radials. Radials (or inferradials) 3, large, making up most of the cup; arm-bearing plates variable in number (7-14), with lateral projections distally; articulating facets flat, radially serated in some specimens (probably due to weathering); pararadials 2-9.

REMARKS. Rozhnov (1981) provided a thorough analysis of the Pisocrinidae in which 2 lineages lead from spherical, low bowl-shaped or low conical *Pisocrinus* with 5 basals to high conical forms with 3 basals, the latter occurring in the Upper Devonian. The lineage leading to *Jaekelicrinus* through *Trichocrinus* and *Calycanthocrinus* is the only one developing pararadials. *Playfordicrinus* also has pararadials and 3 basals but retains the subspherical shape of *Pisocrinus*. It can not be considered part of the *Jaekelicrinus* lineage because that lineage had achieved and stabilised its high conical thecal shape before developing pararadials and the rest of the lineage retains that thecal shape. Likewise the *Triacrinus* lineage developed a high conical thecal shape in

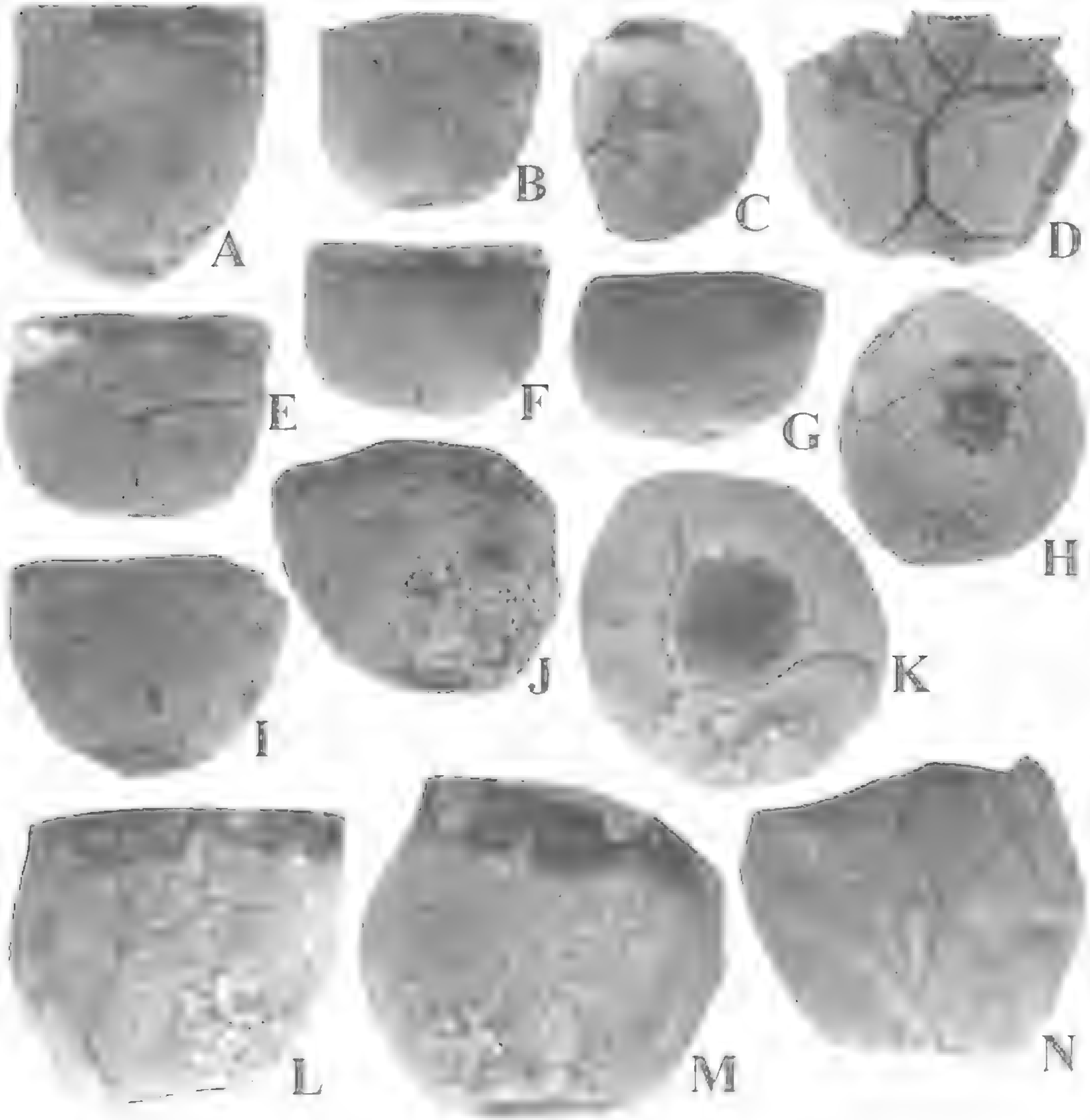


FIG. 21. *Playfordicrinus kellyensis* gen. et sp. nov. all from NMVPL1938. A-D, lateral views except for proximal view C of NMVP100311, ×5, ×3, ×4 and ×5, respectively. E,F-H, lateral views except for proximal view H, of NMVP100312, ×4. I, J, lateral views of NMVP100313, ×4. K-N, proximal (K) and lateral views of NMVP100314, ×5.

the Middle Devonian so *Playfordicrinus* would have to be considered a reversion in thecal shape if attached to that lineage. Cup shape and the fine granular thecal ornament lead us to suggest that *Playfordicrinus* evolved from *Pisocrinus (Granulosocrinus)* in the Middle Devonian and involved the same development of pararadials and reduction to 3 basals as in *Jaekelicrinus* but with retention of the primitive cup shape of *Pisocrinus*. Although our suggestion may not be in accord with cladistic principles because we infer the derived characters of pararadials to have evolved independently twice and reduction in basals from 5 to 3 to have evolved 3 times it is compatible with the phylogeny of the Pisocrinidae as depicted by Rozhnov (1981, fig.9). The new genus is readily distinguished from *Pisocrinus* by its 3 basals and its pararadials

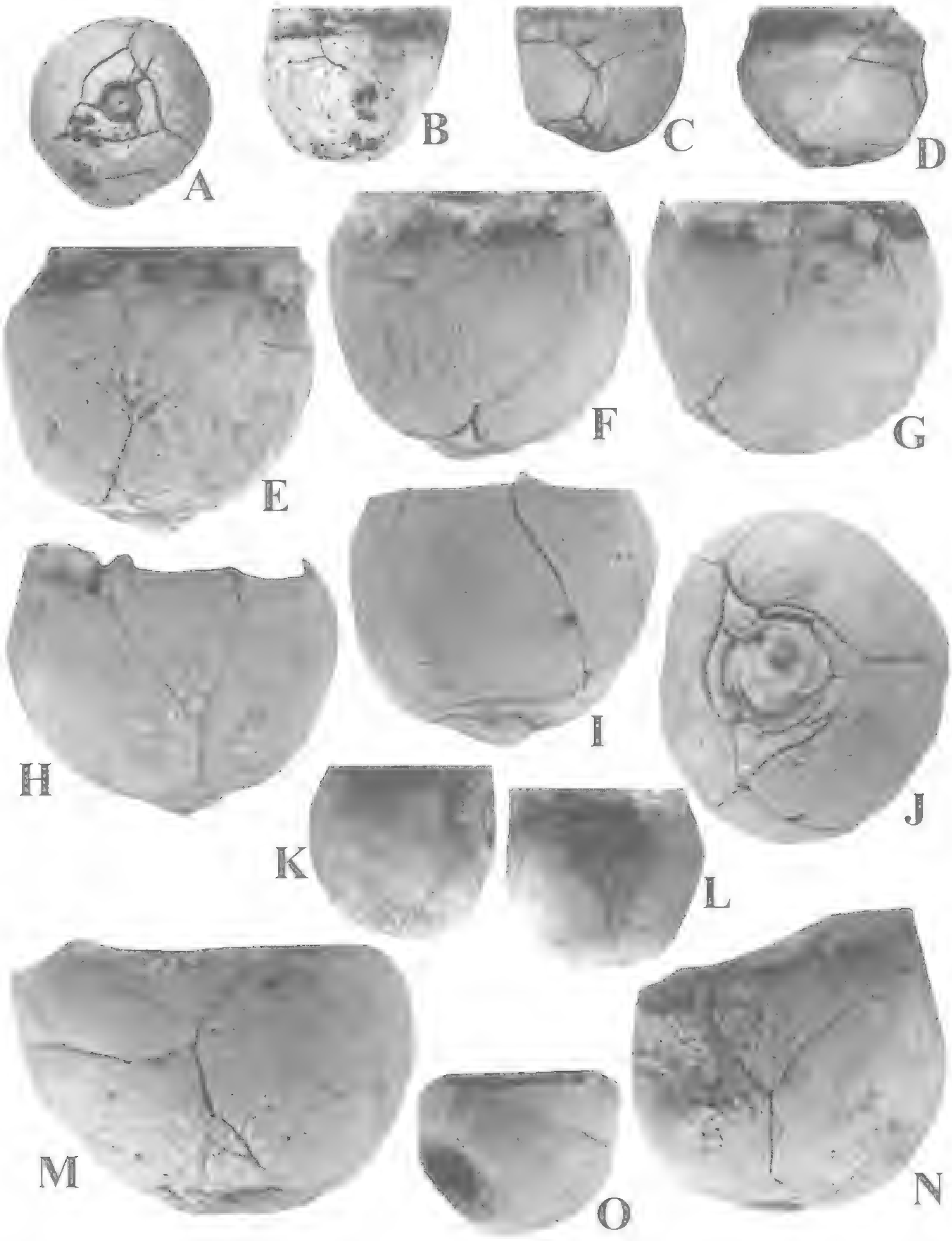


FIG. 22. *Playfordicrinus kellyensis* gen. et sp. nov. all from NMVPL1938 except A-D from NMVPL1936. A-D, proximal (A) and lateral views of QMF36203. A, ×3. B-D, ×4. E-J, proximal (J) and lateral views of holotype NMVP100315, ×8. K, L, N, lateral views of NMVP100316. K, L, ×4. N, ×6. M, O, lateral views of NMVP100317, ×7 and ×4, respectively.

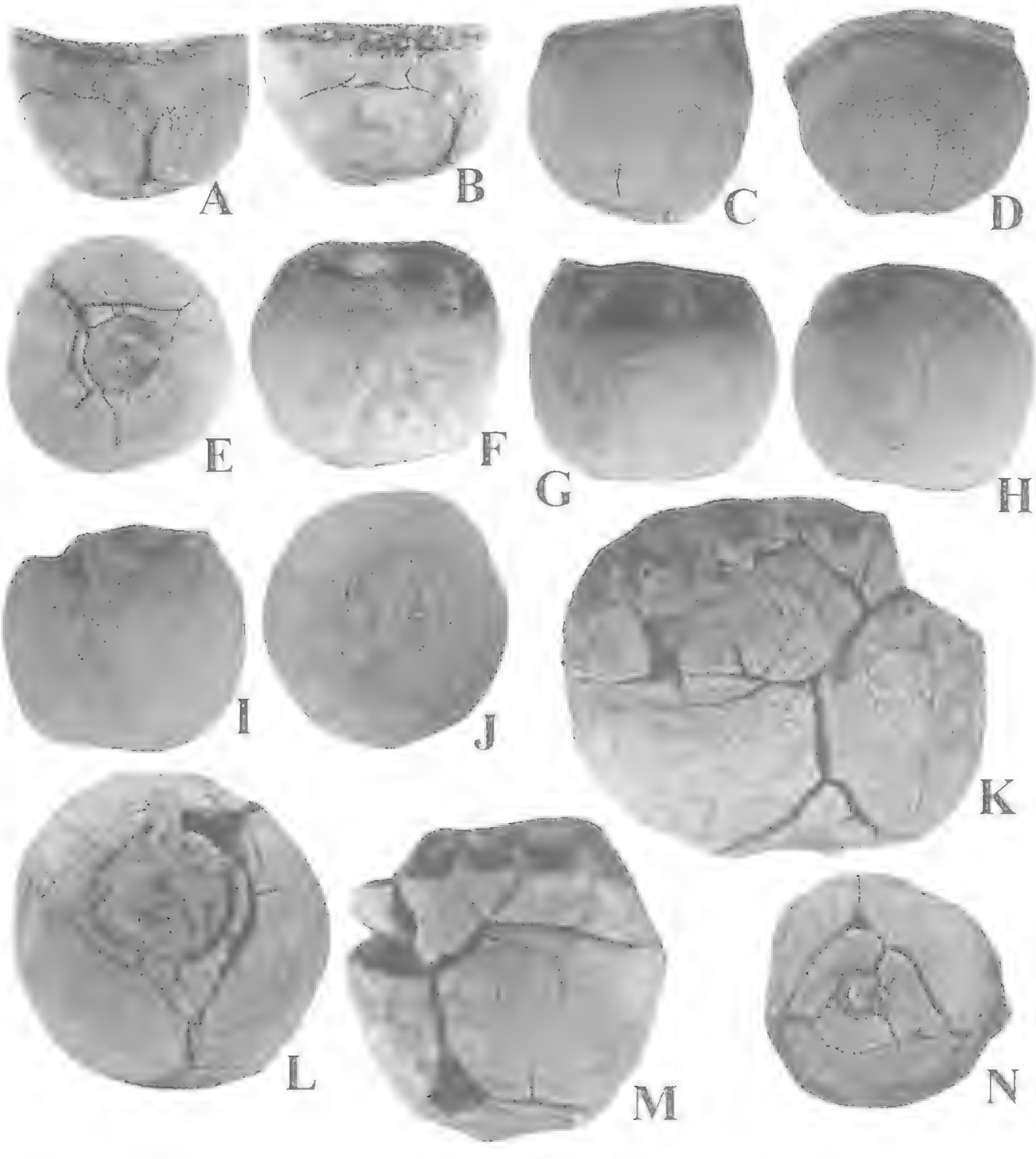

FIG. 23. *Playfordicrinus kellyensis* gen. et sp. nov. all from NMVPL1938. A-E, basal (E) and lateral views of NMVP100318, ×4. E, ×3. F-J, lateral and basal (J) views of NMVP100319, x6. K, N, lateral and basal views respectively of NMVP100320, ×6 and ×3, respectively. L, M, basal and lateral views of NMVP100321, ×6.

and from the other pisocrinids with 3 basals by its subspherical cup. Ausich (1977) and Rozhnov (1981) voiced different opinions on the concept of *Pisocrinus*; the former synonymised *Parapisocrinus* while the latter retained it as a separate genus. This difference of opinion does not affect the discussion (above) leading to erection of a new genus evolving from *Pisocrinus* (*Granulosocrinus*). Settlement of the *Parapisocrinus*

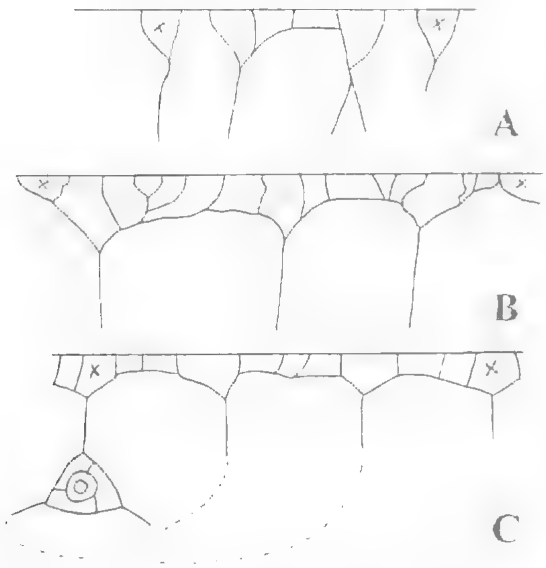


FIG. 24. *Playfordicrinus kellyensis* gen. et sp. nov. Schematic plating arrangement from camera lucida sketches; the 2 marks at either end of each sketch indicate the same plate and thus the full circumference of the cup. A, smallest (5mm long) cup NMVP100319 (Fig. 23F-J) showing 2 radials. B, largest (9mm long) NMVP100318 (Fig. 23A-E) showing all 3 large plates as inferradials. C, schematic with basals shown and indication of relation to inferradials QMF36203 (Fig. 22A-D).

question may modify Rozhnov's (1981) phylogeny but would not change the argument herein.

**Playfordicrinus kellyensis** sp. nov.
(Figs 21-24)

ETYMOLOGY. For Kelly Pass through which access is gained to the type locality.

MATERIAL. Holotype. NMVP100315. Paratypes: NMVP100311-100314, 100316-100321, QMF36203 all from NMVPL1938, S of the Teichert Hills.

DIAGNOSIS. As for genus.

DESCRIPTION. Cup small, up to 10mm in diameter and 9mm long, subspherical, with distal sides becoming straighter (rather than distally incurving) during growth, with fine widely spaced granular ornament; plates very thick, body cavity small. Basals 3, forming subtriangular circlet around large circular attachment facet; each basal slightly curved around stem facet, shaped like a tick (i.e. with a long arm beginning near one interradial suture, expanding into distal projection at next interradial suture and short extension beyond distal projection), with distal projection sometimes reaching as far as point where suture divides distally (thus producing a 4 way sutural junction). Of 3 large plates in cup 1 always inferradial, other 2 may be either radials or inferradials; arm-bearing plates variable in number with growth, 7-14. Smallest specimens (5mm diameter) with 2 large radials, a large inferradial, 2 small radials and 3 pararadials. In largest specimen 3 large plates inferradials, 2 small radials and 12 pararadials. Radial facets almost as wide as plate except for narrow distal projections laterally; each projection paired with another on adjoining plate. In weathered specimens there is a striate comb-like outer lip to facet. Stem circular in section. Arms unknown.

REMARKS. Increasing number of arm-bearing plates and changing thecal shape from subspherical to more straight-sided are trends with growth which may be equated with trends in other lineages in the family. Comparisons of this species within the family are detailed above in the generic remarks.


FIG. 25. Catillocrinid? indet., NMVP100322 from NMVPL1938, proximal (A) and two lateral (B,C) views, ×4.

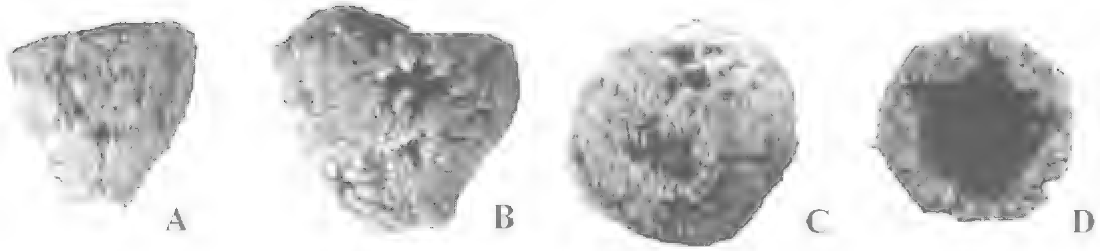


FIG. 26. *Stylocrinus tabulatus* (Goldfuss, 1839), all silicified cups from Frasnian part of Sadler Limestone SW of Wade Knolls, Paddy's Valley. A, C, lateral and proximal views of QMF40372, x3. B, D, lateral and distal views, respectively, of QMF36210, ×3.

Superfamily ALLAGECRINOIDEA Carpenter & Etheridge, 1881
Family CATILLOCRINIDAE Wachsmuth & Springer, 1886

**Catillocrinid**? indet.
(Fig. 25)

MATERIAL. NMVP100322 from NMVPL1936.

DESCRIPTION. Cup 4mm long, 4mm in diameter, conical. Basals 3, with 2 very large and one very small; stem facet large, with marginal crenularium and areola of similar width. Radial circlet unclear in parts, with at least 1 plate not reaching distal margin of cup, with 3 large radials and numerous small ancilliary ones. Distal surface of cup with small central cavity, with larger coarse multiple facets on larger radials and multiple narrow facets and fine intervening ridges on small radials.

REMARKS. This specimen is almost unidentifiable and its assignment to the Catillocrinidae is very tentative. No known catillocrinid has the plate arrangement interpreted in this specimen but the distal surface and the 2 large and 1 tiny basals suggest that family. As no other evidence is available this assignment is made very tentatively.

Superfamily BELEMNOCRINOIDEA S.A. Miller, 1883
Family SYNBATHOCRINIDAE S.A. Miller, 1889

**Stylocrinus** Sandberger & Sandberger, 1856

TYPE SPECIES. *Stylocrinus scaber* Sandberger & Sandberger, 1856 from the Middle Devonian of Germany by monotypy.

**Stylocrinus tabulatus** (Goldfuss, 1839)
(Fig. 26)

MATERIAL. QMF40372 and 36210 from insoluble residue of the Sadler Limestone taken by Alex Cook in 1998 from SE of Wade Knoll in the Paddy's Valley area.

DESCRIPTION. Cup 4mm long, 4mm diameter, low conical, with smooth thick plates. Basals 3, 2 large and 1 small; large ones supporting a radial symmetrically and sutured to 2 others distolaterally. Radials 5, pentagonal, with horizontal distal margin, in distal view thin at centre and thicker at interradial sutures; radial facet peneplenary, with distinct transverse ridge. Arms and stem unknown.

REMARKS. The genus had been restricted to the Middle Devonian of Europe (Schultze, 1867) and Russia (Dubatolova, 1971) but Strimple (1963) added *S. elimatus* from the Silurian Hunton Formation of Oklahoma. However, the distal view of Strimple's specimen shows the radial facet to be reclining on a thick central part of the radial plate (as thick as or thicker than the lateral part at the interradial sutures). This structure is much more reminiscent of *Phimocrinus* Schultze (1867, pl. 3, figs 6a, 7a) whereas the new Australian species with definite invagination at middle of each radial is identical with *Stylocrinus tabulatus* (Schultze, 1867, pl. 3, figs 4a, 5a). A number of subspecies have been identified in *S. tabulatus* (Dubatolova, 1971) but with length = width the Australian specimens appear intermediate between *altus* (length > width) and *depressus* (width > length). We thus assign them to the broader species concept.

When Teichert (1949) identified *Storthingocrinus* there is a distinct possibility that he had material of this species because the plating arrangement is identical; however, the radial facets of

*Storthingocrinus* are quite different and it has been suggested that it is a camerate crinoid (Prokop & Petr, 1997).

Subclass CLADIDA Moore & Laudon, 1943
Family CODIACRINIDAE Bather, 1890

**Codiacrinus** Schultze, 1867

TYPE SPECIES. *Codiacrinus granulatus* Schultze, 1867 from the Middle Devonian of Germany; by original designation.

REMARKS. This genus was discussed by Jell (in Jell & Holloway, 1983:16); it contains 7 species, *C. granulatus*, *C. schultzei* Follmann, 1887, *C. procerus* (Prokop, 1973), *C. ornatus* (Prokop, 1973) (probably a junior synonym of *C. granulatus*), *C. rarus* Jell in Jell & Holloway, 1983, *C. nicolli* sp. nov. and *C. secundus* Jell, 1999.

**Codiacrinus nicolli** sp. nov.
(Fig. 27)

ETYMOLOGY. For Robert Nicoll who collected some of the material.

MATERIAL. Holotype: WAM91.710 from QML1929. Paratypes: CPC34566-34577 from section 354 (9m level) on W side of McWhae Ridge (Nicoll & Playford, 1993). Other Material: QMF36204-36206 from QML1031, E side of Bugle Gap S of Wagon Pass.

DIAGNOSIS. Cup small, with granular ornament but no ray ridges; basals small, pentagonal, almost equidimensional, with proximal margin shorter than others; radials long, with angustary radial facets, with strong distal projections both sides of facet.

DESCRIPTION. Cup small, up to 11mm long and 8mm diameter, subglobose to subcylindrical, with broadly flared basal circlet, of very thick plates (body cavity less than 1/2 thecal diameter). Infrabasals 3 (in Fig. 22E there appear to be only 2, but it is a weathered base and the positions of the visible sutures suggest that the 3rd suture has been fused and thus the specimen aberrant), 2 large and equal and 1 small, separated by sutures in typical Y-shaped arrangement, with obtuse angle distally at base of sutures between basal plates, outflared away from stem. Basals pentagonal, with 4 equal sides and shorter proximal margin, up to 4mm across. Radials large, longer than wide, occupying most of theca; radial facet angustary, more than 1/2 radial width, subrectangular excavation into radials, with flat semicircular floor and convex butterfly-shaped inner surface, with lateral parts of radials of adjoining plates forming 5 projections distally. No anal plates in theca. Stem circular in section, very small diameter, with fine central lumen. Arms unknown.

REMARKS. Smaller size, type of radial facet, small infrabasal circlet, outflared infrabasal and basal circlets and stem diameter much less than that of cup distinguish this species within the genus. It is probably most similar to the type species particularly in comparison with Schultze's (1867, pl. 3, fig. 9C) second specimen which is more cylindrical than globose. It is quite distict from the other Australian species in the Pridoli and Lochkov of Victoria in its stem size, size of infrabasals, radial facets and ornament.

Subclass FLEXIBILIA Zittel, 1895
Order TAXOCRINIDA Springer, 1913
Superfamily TAXOCRINOIDEA Angelin, 1878
Family TAXOCRINIDAE Angelin, 1878

?**Taxocrinus** sp.
(Fig. 28D)

MATERIAL. QMF40360 from QML1031.

DESCRIPTION. Cup plates smooth. Infrabasals 3, azygous in C ray, visible externally, forming narrow margin to stem facet. Basals 5, pentagonal, equidimensional except posterior one; posterior basal much longer than others and also wider, hexagonal, with distal margin weathered and unclear but apparently with distal lateral corners curving towards axis of cup around a central semicircular part of margin that could be part of an aperture that may lead into an anal tube.

REMARKS. This basal cup fragment is too incomplete for species identification. The distal end of the posterior basal suggests the beginning of a tubular structure as in an anal tube suggesting the Taxocrinidae. Within that family, *Taxocrinus* Phillips in Morris, 1843, which ranges from the Middle Devonian to Lower Carboniferous of Europe and North America, has a symmetrical posterior basal leading directly into an anal tube and also has the stem facet restricted to the infrabasal circlet. However, it is retained in open nomenclature because it is so incomplete.

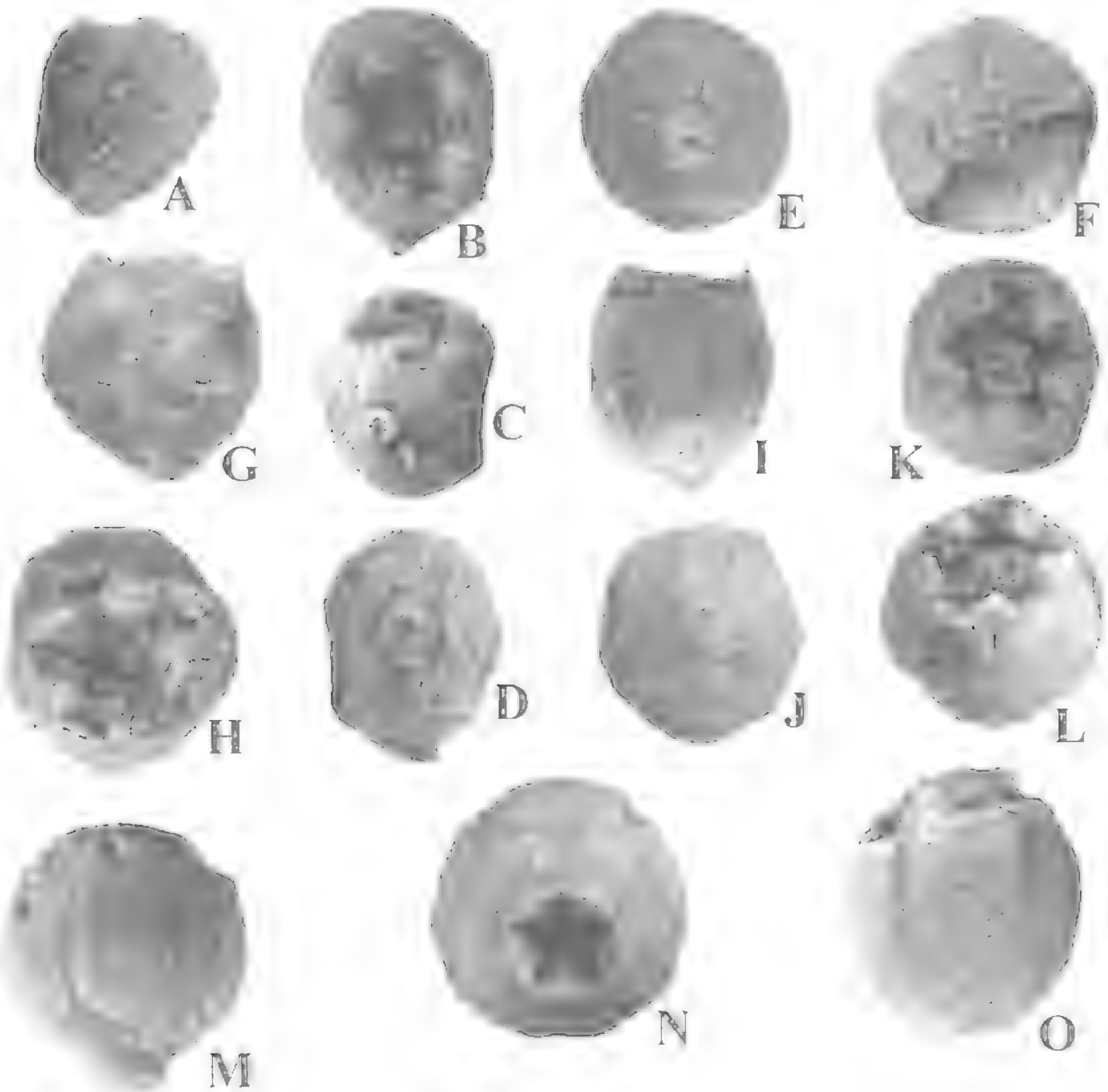


FIG. 27. *Codiacrinus nicolli* sp. nov. all from WCB354/9 (Nicoll & Playford, 1993) except M from QML1029 and N, O from QML1031. A-D, CPC34566. ×3. A, lateral view. B, distal view. C, oblique lateral view. D, proximal view. E, proximal view of CPC34567, ×3. F, distal view of broken theca showing thickness of shell. CPC34568, ×3. G, lateral view of CPC34569, x3. H, distal view of CPC34570, ×3. I,J, lateral and proximal views of CPC34571, ×3. K,L, distal and oblique views of CPC34572, ×3. M, lateral view of WAM91.710, ×7. N, O, proximal and lateral views of QMF36204, ×5.

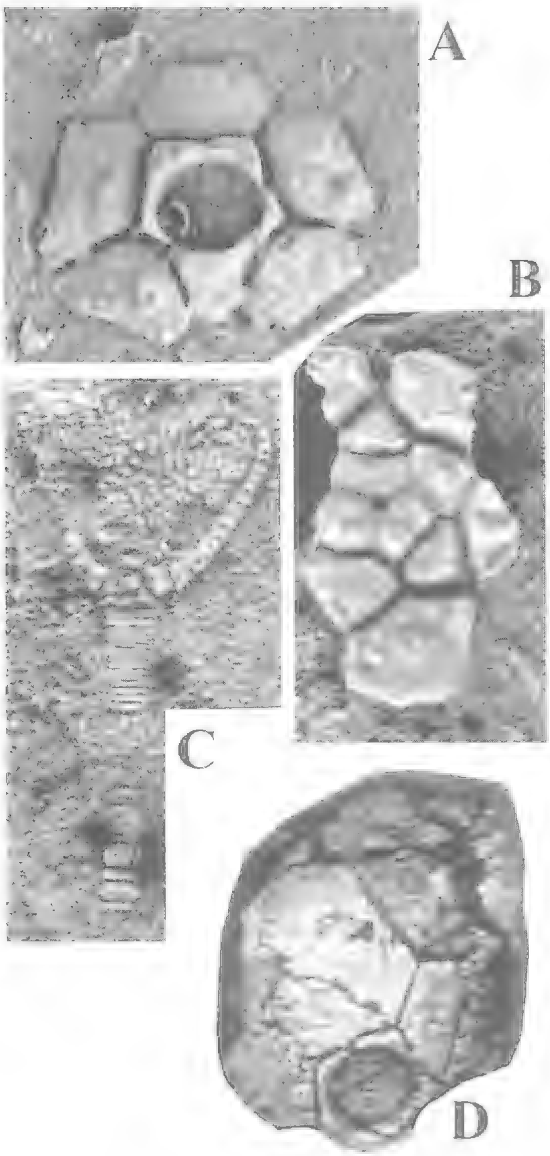

FIG. 28. A-C, *Forbesiocrinus* sp. A, proximal view of basal and radial circlets, NMVP100323 from NMVPL1930, ×4. B, internal view of base of cup showing infrabasal, basal and radial circlets, NMVP100324 from NMVPL1929, ×4. C, weathered section through whole animal showing differentiated stem and strongly incurved and coiled arms, QMF36207 from the Virgin Hills Formation W of Hull Range, ×2. D, ?*Taxocrinus* sp., basal view of cup fragment with infrabasal circlet visible around stem facet and large posterior basal at upper left QMF40359 from QML1031, ×4.

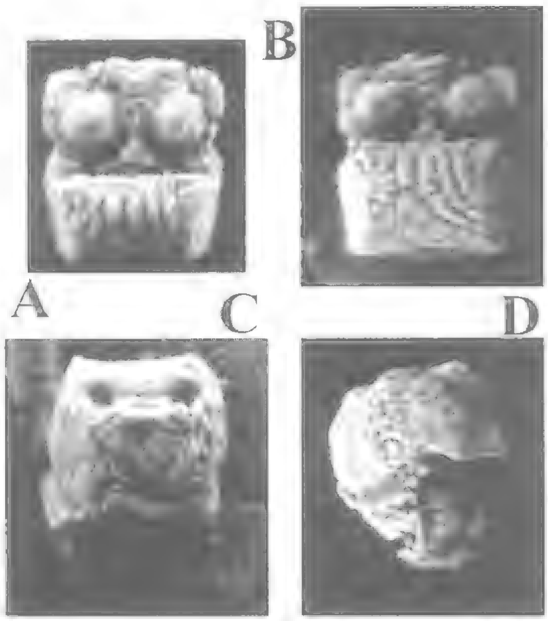

FIG. 29. Cyclocystoid indet., silicified marginal ossicle, QMF36209, ×3, from Frasnian part of Sadler Limestone SW of Wade Knolls, Paddy's Valley. A, B, ventral views of marginal ossicle tilted slightly differently to show the cupule zone and entries to radial ducts (A) and crest (B) more clearly. C, dorsal view showing entries to radial ducts. D, lateral view showing high rounded crest, cupule zone and circumferential canal.

Order SAGENOCRINIDA Springer, 1913
Superfamily SAGENOCRINOIDEA Roemer, 1854
Family SAGENOCRINITIDAE Roemer, 1854

**Forbesiocrinus** sp.
(Fig. 28A-C)

MATERIAL. NMVP100323 from NMVPL1930 and NMVP 100324 from NMVPL1929 and probably QMF36207 from the Virgin Hills Formation W of the Hull Range.

DESCRIPTION. Cup with flat base, plates with tuberculate ornament. Infrabasals 3, equal, pentagonal, concealed within stem facet. Basals 5, pentagonal, with only distal triangular tips visible laterally forming margin to stem facet; posterior basal with an extra side distally, supporting 2 anal plates, separating C and D radials. Radials 5, hexagonal, in contact with each other except in posterior interray; radial facet plenary. Stem tapering slightly distally, of extremly short columnals proximally, becoming heteromorphic

(alternating long and short columnals with angular latus) distally.

REMARKS. Assignment to *Forbesiocrinus* is based on the posterior basal supporting 2 anal plates apparently symmetrically but the lack of arms prevents meaningful comparison with other species of the genus. The specimen in section from the Hull Range is doubtfully referred to this taxon but if correctly interpreted has the infrabasals completely concealed by the stem facet. In the other known flexible crinoid from the basin the infrabasals are evident laterally.

Class CYCLOCYSTOIDEA
Miller & Gurley, 1895
Family CYCLOCYSTOIDIDAE
S.A. Miller, 1882

**Cyclocystoid** indet.
(Fig. 29)

MATERIAL. QMF36209 from the Frasnian part of the Sadler Limestone SW of Wade Knolls in Paddy's Valley.

DESCRIPTION. Single marginal ossicle 1mm wide, 2mm in radial length and 1mm high, with bevelled lateral margins indicating that the marginal ossicles were not in contact throughout their lateral margins. Crest high, with almost circular lateral profile, with ornament of rounded (in section) ridges aligned in parallel curves across crest. Cupule zone with 2 circular cupules each with strong circular central tubercle, with sharp ridge between cupules, with narrow deep circumferential channel, with 2 relatively large radial ducts from centre of each cupule. Dorsal surface smooth.

REMARKS. The features of this ossicle are clearly in line with the Cyclocystoidea (Smith & Paul, 1982) but within the class it does not appear to fit any genus. The youngest described genus is *Sievertsia* last known from the Middle Devonian of Europe but that genus has flat or concave crests and dorsal surfaces and cannot accept the Australian ossicle. The ornament on the crest is unknown in any genus and this ossicle probably represents a new genus but it is retained in open nomenclature pending more complete material. Smith & Paul (1982: 677) reported an occurrence of the class in the Frasnian of Iowa, communicated to them by Terry Frest (pers. comm. 1980) but without illustration comparison is not possible. However, the occurrences in Iowa and Western Australia are the youngest known occurrences of the class and are valuable knowledge for that reason.

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LITERATURE CITED

AUSICH, W.I. 1977. The functional morphology and evolution of *Pisocrinus* (Crinoidea: Silurian). Journal of Paleontology 51: 672-686.

BECKER, R.T. & HOUSE, M.R. 1997. Sea-level changes in the Upper Devonian of the Canning Basin, Western Australia. Courier Forschungen-Institut Senckenberg 199: 129-146.

BECKER, R.T., HOUSE, M.R. & KIRCHGASSER, W.T. 1993. Devonian goniatite biostratigraphy and timing of facies movements in the Frasnian of the Canning Basin, Western Australia. Geological Society Special Publication 70: 293-321.

BREIMER, A. & DOP, J.A. 1975. An anatomical and taxonomic study of some Lower and Middle Devonian blastoids from Europe and North America. 1 and 2. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, 78: 39-61.

BREIMER, A. & MACURDA, D.B. 1972. The phylogeny of the fissiculate blastoids. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Naturkunde, Eerste Reeks 26(3): 1-390.

BRIGGS, D.E.G. & ROLFE, W.D.I. 1983. New Concavicarida (New Order: ? Crustacea) from the Upper Devonian of Gogo, Western Australia and the palaeoecology and affinities of the group. Special Papers in Palaeontology 30: 249-276.

BROWER, J. 1967. The actinocrinitid genera *Abactinocrinus*, *Aacocrinus* and *Blairocrinus*. Journal of Paleontology 41: 675- 705.

COCKBAIN, A.E. 1984. Stromatoporoids from the Devonian reef complexes, Canning Basin, Western Australia. Geological Survey of Western Australia Bulletin 129: 1-108.

DRUCE, E.C. 1976. Conodont biostratigraphy of the Upper Devonian reef complexes of the Canning Basin, Western Australia. Bulletin of the Bureau of Mineral Resources, Geology and Geophysics 158: 1-303.

DUBATOLOVA, Yu. A. 1964. Morskii lilii devona Kuzbassa [Devonian crinoids of the Kuznetz

Basin]. Akademiya Nauk SSSR, Sibirskoe Otdeleniye Trudy Instituta Geologii i Geofiziki 153p, 14pl.

1971. Morskie lilii Rannego i Crednego Devona Altay i Kuzbassa. [Crinoids of the Early and Middle Devonian of the Altay and Kuzbass.] Akademia Nauk SSSR, Sibirskoe Otdelenie Trudy Instituta Geologii i Geofiziki 124: 1-159.

ETHERIDGE, R. Jr & CARPENTER, P.H. 1886. Catalogue of the Blastoidea in the Geological Department of the British Museum (Natural History), with an account of the morphology and systematics of the group, and a revision of the genera and species. (British Museum (Natural History): London).

FAY, R.O. 1961. Blastoid studies. The University of Kansas Paleontological Contributions, Echinodermata, Article 3: 1-147.

FOLLMANN, O. 1887. Unterdevonische Crinoiden. Verhandlungen des naturhistorischen Vereines der preussischen Rhinelande, Westfalens und des Reg.-Bezirks Osnabruck, Vierundvierzigster Jahrgang 4: 113-138.

GLENISTER, B.F. 1958. Upper Devonian ammonoids from the *Manticoceras* Zone, Fitzroy Basin, Western Australia. Journal of Paleontology 32: 58-96.

GLENISTER, B.F. & KLAPPER, G. 1966. Upper Devonian conodonts from the Canning Basin, Western Australia. Journal of Paleontology 40: 777-842.

GOLDFUSS, G.A. 1831. Petrefacta Germaniae. Vol 1, Part 2, Radiariorum reliquiae, pp. 115-221. (Arnz & Co: Dusseldorf).

1839. Bietrage zur Petrefactenkunde Acta Naturae. Curiosorum. Nova Acta Physico-medica Academie Caesar Leopoldino-Carolinae Naturae Curiosorum 19: 329-364.

HILL, D. & JELL, J.S. 1970. Devonian corals from the Canning Basin, Western Australia. Geological Survey of Western Australia Bulletin 121: 1-158.

HOROWITZ, A.S., MACURDA, J.B. & WATERS, J.A. 1986. Polyphyly in the Pentremitidae (Blastoidea, Echinodermata). Bulletin of the Geological Society of America 97: 156-161.

JELL, P.A. 1999. Silurian and Devonian crinoids from central Victoria. Memoirs of the Queensland Museum 43: 1-114.

JELL, P.A. & HOLLOWAY, D.J. 1983. Devonian and ?Late Silurian palaeontology of the Winneke Reservoir site, Christmas Hills, Victoria. Proceedings of the Royal Society of Victoria 95: 1-21.

JELL, P.A., JELL, J.S., JOHNSON, B.D., MAWSON, R. & TALENT, J.A. 1988. Crinoids from Devonian limestones of eastern Australia. Memoirs of the Queensland Museum 25: 355-402.

KESLING, R.V. 1964. A new species of *Melocrinites* from the Middle Devonian Bell Shale of Michigan. Contributions from the Museum of Paleontology, University of Michigan 19: 89-103.

LANE, N.G., WATERS, J.A. & MAPLES, C.G. 1997. Echinoderm faunas of the Hongguleleng Formation, Late Devonian (Famennian), Xinjiang-Uygur Autonomous Region, People's Republic of China. Paleontological Society Memoir 47: 1-43 (Journal of Paleontology 71(2), supplement).

LONG, J.A. 1991. The long history of Australian fossil fish. Pp. 337-428. In Vickers-Rich, P., Monaghan, J.M., Baird, R.F. & Rich, T.H. (eds) Vertebrate palaeontology of Australasia. (Pioneer Design Studio: Melbourne).

MOORE, R.C. & TEICHERT, C. (eds) 1978. Treatise on invertebrate paleontology. Part T. Echinodermata 2. 3 vols. (Geological Society of America & University of Kansas: Lawrence, Kansas).

MORRIS, J. 1843. A catalogue of British fossils. Comprising all the genera and species hitherto described; with reference to their geological distribution and to the localities in which they have been found. (John van Voorst: London).

MULLER, J. 1856. Über neue Crinoiden aus dem Eifeler Kalk. Koniglich Akademie des Wissenschaft Berlin. Monatsbericht 1856: 353-356.

NICOLL, R.S. & PLAYFORD, P.E. 1993. Upper Devonian iridium anomalies, conodont zonation and the Frasnian-Famennian boundary in the Canning Basin, Western Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 104: 105-113.

PETERSEN, M.S. 1975. Upper Devonian (Famennian) ammonoids from the Canning Basin, Western Australia. Paleontological Society Memoir 8: 1-55. (Journal of Paleontology 49(5), Supplement).

PHILLIPS, J. 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and west Somerset. (Longman, Brown, Green & Longmans: London).

PLAYFORD, P.E. 1981. Devonian reef complexes of the Canning Basin Western Australia. Field Excursion Guidebook, Fifth Australian Geological Convention, Perth. 44p. (Geological Society of Australia: Sydney).

PLAYFORD, P.E. & LOWRY, D.C. 1966. Devonian reef complexes of the Canning Basin, Western Australia. Geological Survey of Western Australia Bulletin 188: 1-150.

PROKOP, R.J. 1973. *Elicrinus* n. gen. from the Lower Devonian of Bohemia (Crinoidea). Vestnik Ustredniho Ustavu Geologickeho 48: 221-224.

PROKOP, R.J. & PETR, V. 1997. The genus *Pygmaeocrinus* Bouska, 1947 (Crinoidea, Inadunata) in the Devonian of the Barrandian area (Czech Republic). Acta Musei Nationalis Pragae, Series B, Historia Naturalis 53: 1-10.

REIMANN, I.G. 1945. New Devonian blastoids. Bulletin of the Buffalo Society of Natural Sciences 19(2): 22-43.

RIGBY, J.K. 1986. Late Devonian sponges of Western Australia. Geological Survey of Western Australia Report 18: 1-59.

ROEMER, C.F. 1852. Bietrage zur geologischen Kenntnis des nordwestlichen Harzgebirges. Palaeontographica 3(2): 69-111.

1855. Erste Periode, Kohlen-Gebirge. In Bronn, H.G. Lethaea Geognostica, vol. 2 (3rd ed.) (E. Schweizerbart: Stuttgart).

ROZHNOV, S. 1981. Morskie lilii nadcemeistva Pisocrinacea [Sea lilies of the Superfamily Pisocrinacea]. Trudy Paleontological Institute 192: 1-127.

SANDBERGER, G. & SANDBERGER, F. 1856. Die Versteinerungen des rheinischen Schichtensystems in Nassau. (Kreidel & Niedner: Wiesbaden).

SCHULTZE, L. 1867. Monographie der Echinodermen des Eifler Kalkes. Denkschriften der kaiserlichen Akademie der Wissenschaft. Mathematisch-Naturwissenschaftliche Classe 26: 113-230.

SEDDON, G. 1970. Frasnian conodonts from the Sadler Ridge-Bugle Gap area, Canning Basin, Western Australia. Journal of the Geological Society of Australia 16: 723-753.

SMITH, A.B. & PAUL, C.R.C. 1982. Revision of the Class Cyclocystoidea (Echinodermata). Philosophical Transactions of the Royal Society of London B. Biological Sciences 296: 577-684.

SPRINGER, F. 1920. The Crinoidea Flexibilia. Smithsonian Institution Publication 2501: 1-486.

STRIMPLE, H.L. 1963. Crinoids of the Hunton Group. Oklahoma Geological Survey Bulletin 100: 1-169.

STRIMPLE, H.L. & LEVORSON, C.O. 1973. Additional crinoid specimens from the Shellrock Formation (Upper Devonian) of Iowa. Proceedings of the Iowa Academy of Sciences 80: 182-184.

TALENT, J.A., MAWSON, R., ANDREW, A.S., HAMILTON, P.J. & WHITFORD, D.J. 1993. Middle Palaeozoic extinction events: faunal and isotopic data. Palaeogeography, Palaeoclimatology, Palaeoecology 104: 139-152.

TEICHERT, C. 1949. Observations on stratigraphy and palaeontology of Devonian, Western Portion of Kimberley Division, Western Australia. Report of the Bureau of Mineral Resources, Geology and Geophysics 2: 1-55.

THOMAS, A.O. 1924. Echinoderms of the Iowa Devonian. Iowa Geological Survey Annual Reports 1919 and 1920 29: 385-552.

UBAGHS, G. 1978. Camerata. Pp. T408-T519. In Moore, R.C. & Teichert, C. (eds) Treatise on Invertebrate Paleontology. Part T. Echinodermata 3. (Geological Society of America & University of Kansas: Boulder & Lawrence, Kansas).

VEEVERS, J.J. 1959. Devonian brachiopods from the Fitzroy Basin, Western Australia. Bureau of Mineral Resources, Geology and Geophysics Australia Bulletin 45: 1-220.

WATERS, J.A. 1988. The evolutionary palaeoecology of the Blastoidea. Pp. 215-230. In Paul, C.R.C. & Smith, A.B. (eds) Echinoderm phylogeny and evolutionary biology (Clarendon Press: Oxford).

WATERS, J.A. & HOROWITZ, A.S. 1993. Ordinal-level evolution in Blastoidea. Lethaia 26: 207-213.

WHITEAVES, J.F. 1887. On some fossils from the Hamilton Formation of Ontario, with a list of the species at present known from that formation and province. Contributions to Canadian Palaeontology 1: 91-125.

YAKOVLEV, N.N. 1949. *Jaekelicrinus bashkivicus* n. gen., n. sp. Journal of Paleontology 23: 435.

## APPENDIX

### Localities Register

NMVPL1929. From more westerly of 2 stromatolitic limestone horizons mapped by Druce (1976, fig. 29) and Playford (1981, fig. 34) east of Millard Creek, 400-500m E of McWhae Ridge; collection made over 200m of strike 200-400m NNE of line of Section 4 of Druce (1976, fig. 29). Just NE of prominent westerly swing of creek this bed makes low ridge just above creek bank then after crossing creek outcrop area widens as its surface is exposed on low rising ground. GR4160 - 926262.
Age: Although Druce (1976, fig. 29) mapped only 2 stromatolite horizons in his section 4 he mentioned 3 such beds in his text (Druce, 1976: 11). His first stromatolite bed is presumably west of Millard Creek and not mapped; his second stromatolite bed is the first stromatolite bed of Playford (1981: 42) based on the assigned ages 'upper *Palmatolepis triangularis*' zone (Druce, 1976: 11) and 'immediately above the Frasnian-Famenian boundary' (Playford, 1981: 42).
Fauna: *Jaekelicrinus murrayi*, *Forbesiocrinus* sp.

NMVPL1930. From more easterly (i.e. younger) of two stromatolitic limestone horizons mentioned in siting NMVPL1929 and collecting from along a similar strike distance (200m) due E of that mentioned above for NMVPL1929. This horizon forms prominent line of ridges with E dip slope of 10-20 and W scarp over which Casey Falls pour. GR4160 - 926262.
Age: *Palmatolepis quadrantinodosa* Conodont Zone of Druce, (1976: 11) or lower *marginifera* Conodont Biozone (Becker & House, 1997, fig. 9).
Fauna: *Jaekelicrinus murrayi*, *Forbesiocrinus* sp.

NMVPL1931 (= UQL3395 = GSWA21939 = QML1030). From red muddy carbonates of Virgin Hills Formation on left bank of creek above Casey Falls extending from near top of ridge of second stromatolite horizon E to sharp southerly bend in creek; collections from 30-40m of section almost immediately above stromatolite horizon. GR4160 - 926258. GPS location 18

Age: *Palmatolepis quadrantinodosa* Conodont Zone of Druce (1976: 12). Petersen (1975) assigned an age of do II within the *Cheiloceras* zone. This horizon equates to the 'sponge garden facies' of Becker & House (1997: 140, figs 7, 8) which they place in the *Pernoceras delepenei* Goniatite Biozone in the upper *marginifera* Conodont Biozone.
Fauna: *Wacrinus caseyensis*, *Wacrinus millardensis*.

NMVPL1938 (=K190). On GSWA track from Kelly's Pass to Teichert Hills 200-300m N of 90 turn from E to N

just NE of small prominent outlier of Permian Grant Formation (Playford, 1981, fig. 29; Playford & Lowry, 1966, plate 4); low lime knoll with some stromatolites. GR4160 - 933300.
Age: Petersen (1975;53) assigned a probable age of do II and this equates to the late *crepida* or early *rhomboidea* Conodont Biozones which accords with the co-occurring goniatites.
Fauna: *Playfordicrinus kellyensis*.

NMVPL1936 (=K177). At first bend in creek downstream from spring due S of Teichert Hills (Playford & Lowry, 1966, plate 4). Rubbly outcrop above stromatolitic horizon. GR4160 - 942301.
Age: *Palmatolepis rhomboidea* Conodont Biozone (do II) (Glenister & Klapper, 1966: 838).
Fauna: *Jaekelicrinus murrayi*, *Playfordicrinus kellyensis*, holdfasts, Catillocrinid indet.

NMVPL1939. 200-300m SSW of Millard Creek at S end (slightly W) of McWhae Ridge on ridge on left bank of minor left bank tributary marked by Druce (1976, fig. 29); 20m below base of Bugle Gap Limestone. GR4160 - 920256.
Age: At level of *Maenoceras* Lsts (Becker & House, 1997, fig. 7) assigned to the lower *marginifera* Conodont Biozone.
Fauna: *Wacrinus millardensis*, *Jaekelicrinus murrayi*.

QML1031 (=NMVPL1940, = BC23-3 of Seddon (1970), = T66 of Teichert (1949), = site of section 12 of Druce (1976)). On top of most southerly of 5 low hills stretching in a line (for about 1.5 km) SSW from Waggon Pass in Bugle Gap. GR4160 - 905355. GPS location 18

Age: Michael House (pers. comm.) assigns this locality to the *Crickites lindneri* Goniatite Biozone (Becker & House, 1997, fig. 8) which equates to the *linguiformis* Conodont Biozone.
Fauna: *Hexacrinites brownlawi*, *Codiacrinus nicolli*, *Hyperoblastus buglensis*, *Jaekelicrinus murrayi* and *Taxocrinus* sp.

NMVPL1942 (= BC44-1 of Seddon (1970, p. 746)). From section at N end of Ngumban Cliff (Playford, 1981, fig. 29) (i.e. E wall of S entrance to Bugle Gap, just N of Pinnacle Spring). Collection from some 40-50 m of section above lower stromatolite horizon. GR4160 - 891241.
Age: Druce (1976, p. 16), in his Section 25, which is probably a parallel section, dated the lower stromatolite horizon in the *Palmatolepis crepida* Conodont Biozone (do II) and the second stromatolite horizon in the basal *P. quadrantinodosa* Biozone (do II). Very likely the *rhomboidea* Conodont Biozone.
Fauna: *Wacrinus millardensis*, crinoid stems in stromatolites.

NMVPL1950-1956 (=T16 = WAPET H K495). Section between Margaret River and NeedleEye Rocks on first left bank tributary of first left bank creek from Margaret River N of Mount Pierre (Mount Pierre Creek); well exposed silty carbonates with cleaner limestone beds standing up above general outcrop near base. GR4061 - 042783 to 024776.
0-110m no fossils
18 A (= 1950) - 110-147m
18 B (= 1951) - 147-155m *Jaekelicrinus murrayi*, holdfasts.
18 C (= 1952) - 195-210m *Jaekelicrinus murrayi*, holdfasts.
18 D (= 1953) - 210-232m
18 E (= 1954) - 372m
31 F (= 1955) - 382m
31 G (= 1956) = last 10m of section beneath first prominent grey limestone bench on NE side of Needle Eye Rocks; in head of gully opening to SE.
Age: Most of the WAPET H section belongs to the *Pseudoclymenia australis* Ammonoid Biozone (Thomas Becker pers. comm. 1997) which equates to the lower *trachytera* Conodont Biozone (Becker & House, 1997, fig. 8).

QML1029. In bank of Millard Creek slightly N of W from Casey Falls, on the line of section B-C on figure 33 of Playford (1981;35). GPS location 18 44.07'S, 126 05.18'E.
Age: Very late Frasnian, late *Pelmatolepis linguiformis* Conodont Biozone equivalent to the *Crickites lindneri* Ammonoid Biozone (Becker & House, 1997, fig. 9).
Fauna: *Melocrinites solidus* sp. nov., *Codiacrinus nicolli* sp. nov.

# NEW CARBONIFEROUS CRINOIDS FROM EASTERN AUSTRALIA

GARY D. WEBSTER AND PETER A. JELL

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New crinods are described from the Carboniferous of Queensland and New South Wales. Early Carboniferous faunas are dominated by actinocrinitids and platycrinitids. The geographic distribution of *Aacocrinus*, *Dialutocrinus*, *Sampsonocrinus*, *Litocrinus*, *Prininocrinus* and *Holcocrinus* is extended with the first report of these genera from Australia. A fauna from the Neerkol Formation of Queensland containing acrocrinids, an euspirocrinid and a scytalocrinid is the first Late Carboniferous fauna recognised from the non-equatorial belt or higher latitudes. New genera and species introduced are *Denarioacrocrinus neerkolensis*, *D.? ornatus*, *Neerkolocrinus typus* and *Kopriacrinus mckellari*. New species described are *Aacocrinus acylus*, *Manillacrinus acanthus*, *Sampsonocrinus cannindahensis*, *Prininocrinus namoiensis* and *Holcocrinus barrabaensis*. A neotype is designated for *Synbathocrinus ogivalis*. Australian Early Carboniferous crinoid faunas are most closely allied to North American faunas, but developed geographically widely separated from them. ❒ *Crinoids, Carboniferous, Queensland, New South Wales.*

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The few Carboniferous crinoids described from Australia have been reported from NSW and Queensland. De Koninck (1878, 1898) reported 5 species from 2 unknown horizons at Burragood and Glen William, NSW. Etheridge (1892) described 3 camerates from the Mirari Limestone at Greenhills and 1 from Chalky Gully, NSW. This was followed by description of camerates and cladids from the 'Gympie Beds' (incorrectly assigned to the Permian initially), Queensland (Etheridge in Jack & Etheridge, 1892). Identifications were based on the broad concepts of taxa at the time and, with few exceptions, were tentative at best.

More recent reports of crinoids are based on moderately to well-preserved calyces and crowns, allowing more detailed identifications based on modern concepts of taxa. These reports have been an actinocrinitid calyx from Swain's Gully (Pickett, 1960), an acrocrinid from the Late Carboniferous of Queensland (McKellar, 1966), a Visean *Physetocrinus* and two unidentified inadunates from Queensland (Campbell & McKellar, 1969), camerates and inadunates from the Goonoo Goonoo Mudstone and Namoi Formation, NSW (Campbell & Bein, 1971) and a glaphyrocrinid and eumorphocrinid from the New England Fold Belt (Lindley, 1979, 1988).

Carboniferous crinoid specimens that have remained undescribed in survey, university, museum and private collections have been drawn together for detailed study. These specimens add significantly to the known diversity and stratigraphic distribution (Table 1) of the Australian faunas. Our purpose is to: 1, describe the available specimens; 2, provide new data or interpretations of some of the earlier described material; and 3, relate all this material to known faunas elsewhere in the world.

## FAUNAL ANALYSIS

We recognise 35 Early and 5 Late Carboniferous crinoids (Table 1) in Queensland and NSW. This does not include taxa based on stem segments, disarticulated cup plates and fragmentary specimens described by de Koninck (1878, 1898), Etheridge (1892) and Etheridge (in Jack & Etheridge, 1892). Several of the taxa in these reports are based on more complete specimens; 3 are accepted and the others are reassigned herein.

Early Carboniferous crinoids are recognised from 5 formations in Qld and 4 or 5 formations in NSW. Late Tournaisian faunas from the Namoi Formation, Goonoo Gonoo Mudstone and Dangarfield Formation of NSW and the Malchi Formation of Qld are considered coeval and all contain 1 or 2 species common to 2 of the formations. No species occurs in all 4 formations. Camerate crinoids are the most diverse forms in each of the faunas and the only crinoids known from the Dangarfield Formation. The Malchi

Formation has the most diverse fauna and includes the only Tournaisian flexible crinoids recognised in Australia.

Visean faunas are from 2 or 3 formations in Qld and 1 in New South Wales. Except for *Aacocrinus* in the Tournaisian or Visean Tellebang Limestone and the Caswell Creek Group, these faunas contain no genera in common. The only non-camerate taxon in these faunas is the disparid *Litocrinus* in the Baywulla Formation.

Camerate calyces and tegmens have also been found in reef talus of the type section of the Early Carboniferous Lion Creek Limestone west of Rockhampton. However, they are weathered, or so fragmentary, that it has been impossible to identify them below family level. At least 5 genera are present, based on cup shapes and plate structures. In situ crinoid holdfasts are present in the reef core, from where the calyces are thought to have been derived.

Campbell & Bein (1971) noted that Australian Early Carboniferous crinoids have more affinity with North American faunas than do the co-occurring brachiopods. However, they also noted that when the interior of many of the brachiopods described from North America become known this difference may not be so great. Recognition of a rhodocrinitid, *Aacocrinus*, *Sampsonocrinus*, *Cribanocrinus*, *Dichocrinus*, *Dialutocrinus*, *Litocrinus*, *Prininocrinus* and *Holcocrinus* in the Early Carboniferous and an acrocrinid and scytalocrinid in the Late Carboniferous of Australia strengthens the crinoid affinities with North America and Europe. *Aacocrinus*, *Cribanocrinus* and *Prininocrinus* were restricted to North America and *Dialutocrinus* to Europe (Lane & Sevastopulo, 1987, 1992).

Ranges for Lower Carboniferous crinoid genera were given in Lane & Sevastopulo (1987, 1992), and the differences in the ranges between North America and Europe were noted along with first and last occurrences. They also pointed out that, although some differences in ranges and origins and extinctions were noted, most were relatively minor and perhaps the result of better definition of the North American genera and sampling artifacts. All of the Australian crinoid genera that are known from North America and Europe are of Tournaisian age, although some of the genera range into the Visean or younger in North America or Europe (Lane & Sevastopulo, 1987, 1990). These genera strongly support a late Tournasian age for the Namoi Formation, Goonoo Gonoo Mudstone, Dangarfield Formation and the Malchi Formation as had been suggested by other invertebrate fossils (Campbell & Bein, 1971; among others).

Camerate crinoids, that evolved rapidly and that are diverse and most abundant in North America during the middle Tournaisian through Visean, are the Rhodocrinitidae, Actinocrinitidae, Batocrinidae, Coelocrinidae, Dichocrinidae and Platycrinitidae (Lane & Sevastopulo, 1987). The Batocrinidae and Coelocrinidae are known only in North America, the others are well represented in equivalent strata in Europe and Russia. Except for the Batocrinidae and Coelocrinidae these families are represented in equivalent strata of eastern Australia, but presently are known from fewer genera than in Europe or North America.

Disparid (Allagecrinidae, Synbathocrinidae) and poteriocrinid (Poteriocrinitidae, Scytalocrinidae, Graphiocrinidae) crinoids are represented in the Early Carboniferous Australian faunas by 1 or 2 genera each. These families are represented in North America and Europe by several genera and underwent rapid diversification during the Early Carboniferous (Lane & Sevastopulo, 1990).

Flexible crinoids are represented by 2 poorly preserved specimens assigned to taxocrinid and sagenocrinid species. Both of these groups are common in the Early Carboniferous of Europe and North America, and they are known in Russian and Chinese faunas (Lane & Sevastopulo, 1990).

Late Carboniferous crinoids in a Westphalian horizon in the Neerkol Formation the Acrocrinidae, Euspirocrinidae and Scytalocrinidae. The Acrocrinidae range from Tournaisian into the Stephanian. Although known from the Early Carboniferous of North America, Europe and Russia, in the Late Carboniferous they are known only from North America where they underwent a rapid diversification (Moore & Strimple, 1969). Euspirocrinids are most common in the Ordovician and Silurian, waning thereafter. They are represented in North America by *Parisocrinus* and *Zygotocrinus* in the Early Carboniferous. The discovery of euspirocrinids in Australia in the Late Carboniferous and Permian (Webster & Jell, this volume) extends their geographic and stratigraphic range. Scytalocrinids are common in Early and Late Carboniferous deposits worldwide.

If all of the reported Early Carboniferous marine fossil occurrences are plotted on biogeographic

reconstructions, such as Bambach (1990), they lie between 45° N and S latitudes, mostly within 30° of the palaeoequator (Campbell & McKellar, 1969). The faunas are equatorial belt organisms and not truly cosmopolitan (Bambach, 1990). On recent plate reconstructions of Early Carboniferous biogeographic regions (Bambach, 1990) Australia is located on the E edge of what was becoming Pangea. Thus, the Australian crinoid faunas evolving in basins along the W border of Panthalassa in the Tournaisian and Visean were well away from the European and North American faunas on the N and W sides of the continental masses, although still in the equatorial belt. A developing Tethys lay to the N and W of the Australian plate. Migration routes and sites of origin are uncertain for many genera at this time (Lane & Sevastopulo, 1987, 1990).

By Westphalian time the Yarrol Shelf of east-central Queensland was between 55° and 60°S latitude. The crinoid fauna of the Neerkol Formation on the Yarrol shelf is the only higher latitude, cooler water, non-equatorial belt fauna known from the Late Carboniferous. The 2 species of acrocrinids in this fauna show greatest affinity with correlative taxa in the midcontinent of North America described by Moore & Strimple (1969). The euspirocrinids (*Kopriacrinus* gen. nov., *Neerkolocrinus* gen. nov.) are an extension of the family into the Late Carboniferous, and the scytalocrinid (*Prininocrinus*) is an extension of a genus previously known from the Early Carboniferous of NW Canada.

## SYSTEMATIC PALAEONTOLOGY

Crinoid teminology follows Moore & Teichert (1978), with columnal patterns after Webster (1974). Measurements are given as: length, parallel to the central axis; width, transverse to, but never cutting or joining the central axis; and depth or thickness, normal to and may join the central axis. Curvature of the cup walls, plate circlets within the cup and fixed brachials are referred to as: incurved if distally bending toward, vertical if parallel to, weakly to strongly flaring if bending away from and horizontal if perpendicular to the central axis.

Material collected by us came from localities entered in the Queenland Museum Locality Register (QML) and is curated in the Queensland Museum Palaeontological Collection (QMF). Other palaeontological collections referred to are indicated by the following prefixes: Geological Survey of Queensland, Brisbane (GSQ); Geological Survey of New South Wales, Lidcombe (MM); Australian National University (ANU) and Australian Museum, Sydney (AMS). Localities are in Queensland unless otherwise noted.

Subclass CAMERATA Wachsmuth & Springer, 1885
Order DIPLOBATHRIDA
Moore & Laudon, 1943
Superfamily RHODOCRINITOIDEA
Roemer, 1855
Family RHODOCRINITIDAE Roemer, 1855

**Rhodocrinitid** gen. nov.
(Fig. 1F)

MATERIAL. QMF38955, QMF38956, locality and horizon unknown, probably Tournaisian Namoi Formation, NSW. Collected by G.M. Philip.

DESCRIPTION. Crown small, 14.3mm long, 5.7mm wide, arms gently splayed. Cup bowl shaped, 5.1mm long, 5.0mm wide, moderately coarse stellate ray ornament, plates moderately inflated. Infrabasals 3?, small, confined to shallow basal cavity. Basals 5?, hexagonal, 1.9mm long, 1.7mm wide, proximally forming base of cup, distally forming base of cup wall, strongly convex transversely and longitudinally. Radials 5?, heptagonal, 1.5mm long, 1.7mm wide, strongly convex transversely and longitudinally. Primibrach 1 hexagonal, 1.1mm long, 1.2mm wide. Primibrach 2 axillary, heptagonal, 1.1mm long, 1.2mm wide. Secundibrach 1 attached to calyx; secundibrach 2 free. All free brachials uniserial, very thick, proximally rectilinear, distally cuneate, narrow, strongly convex transversely, straight longitudinally, with slender pinnule on long side. Secundibrach 4 axillary, no further branching. Arms branching isotomously, 4 in exposed ray, 20 total if all rays branch uniformly. One pinnule per brachial. Pinnulars very slender, elongate, with longitudinal angular ridge, longer than brachials. Interradial series 1-2-2-2-tegmen plates. Tegmen and anals unknown. Stem circular in section, homeomorphic, proximal columnal 0.8mm in diameter. Lumen small, circular; crenularium narrow; latus gently convex.

REMARKS. The crown (Fig. 1F) is flattened with one ray central and part of a second ray along the right side of the specimen. The interray is well-developed, narrowing at the distal end but leaving an obvious gap between the rays at the summit of the fixed arms.

The brachials resemble those of a 4-armed dichocrinid or a primitive poteriocrinitid such as *Liparocrinus*. Most rhodocrinitids have biserial

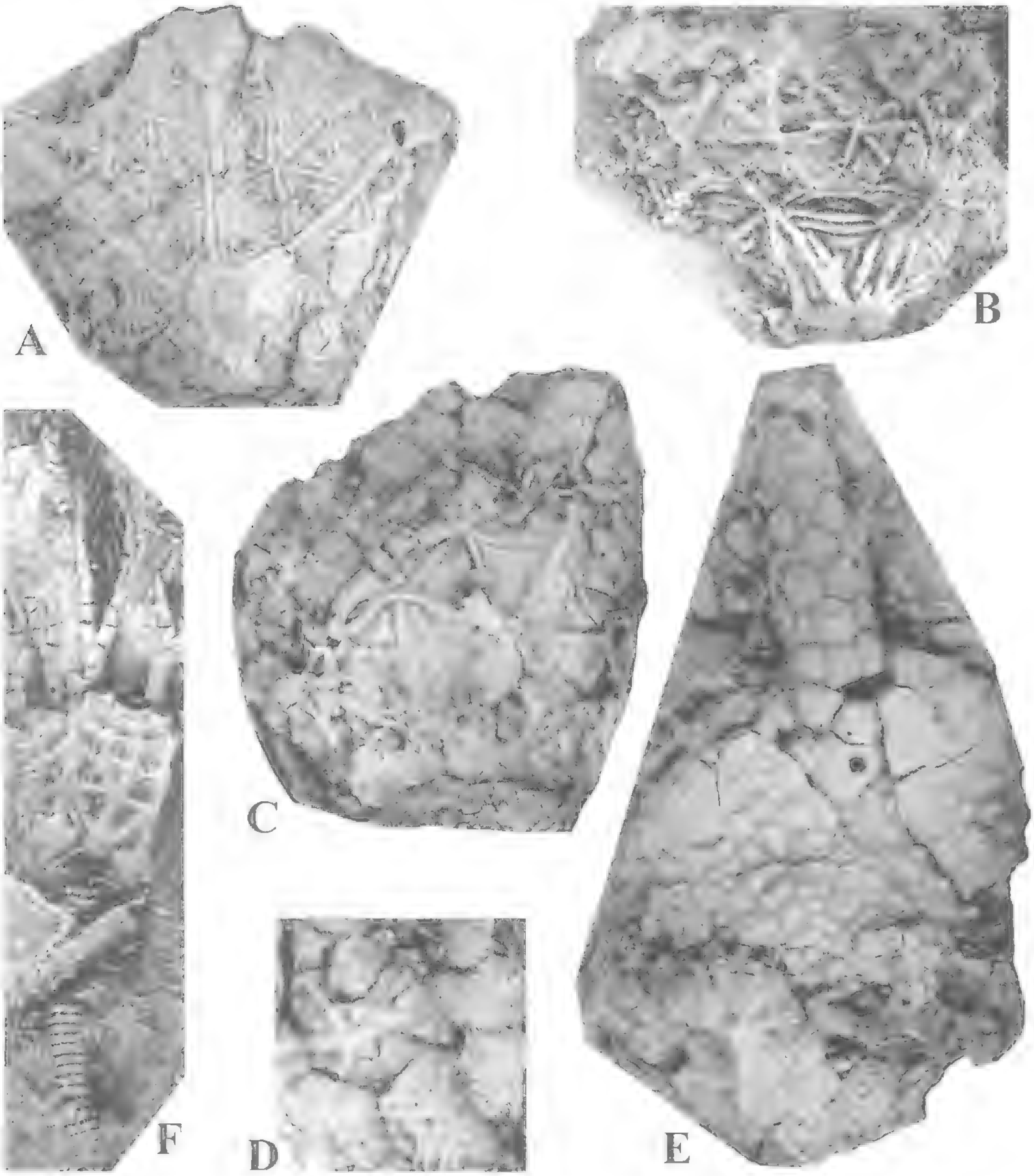



FIG. 1. A-E, *Actinocrinites* sp. 1. A, A ray view of partial calyx QMF38927 ×1.6. B, lateral view of distorted partial calyx QMF38932 ×2.5. C, B ray view of partial calyx QMF38930 ×1.6. D, exterior view of abraded calyx plates QMF38933 ×2.2. E, lateral view of partial theca and tegmen with long anal tube QMF38928 ×2.5. F, Rhodocrinitid gen. nov., lateral view of crown QMF38955 ×4.8.

arms or the uniserial brachials, a primitive condition, are very wide.

The stellate ornament, although known in rhodocrinitids, such as *Diamenocrinus* and *Rhodocrinites*, is not common. The arm branching pattern is slightly advanced as most rhodocrinitids branch on the 2nd secundibrach and then again on the 6th tertibrach or higher and commonly branch one or more times at a higher level. The unfigured specimen (QMF38956) is

crushed, the orientation is uncertain, plate relationships are masked and the ornamentation is only partially preserved.

The specimens may represent a new genus, judged to belong to the rhodocrinitids, but without exposure of the anals, neither specimen is adequate to serve as a holotype. They are associated on a small slab with a scytalocrinid? indeterminate and *Dichocrinus* cf. *D. laudoni*.

Order MONOBATHRIDA
Moore & Laudon, 1943
Superfamily PERIECHOCRINOIDEA Bronn, 1849
Family ACTINOCRINITIDAE Austin & Austin, 1842

REMARKS. Actinocrinitids are among the most common elements in most major Tournaisian or Visean faunas although Visean actocrinitids are relatively rare in Europe. Moore & Laudon (1943) recognised that the actinocrinitids were derived from the periechocrinids and Brower (1967) subdivided them into 4 sections, which were recognised as subfamilies by Ubaghs (in Moore & Teichert, 1978). Brower (1967) also considered the possibility that *Actinocrinites* might be polyphyletic and Campbell & Bein (1971), noting the differences in the arm structure, considered the Eumorphocrininae to be polyphyletic. Webster & Lane (1987) expanded Ubaghs's (in Moore & Teichert, 1978) key to identification of the genera of the Actinocrinitidae to include taxa introduced between 1978 and 1987.

We recognise that the present classification needs revision and does not reflect the phylogeny of a family that is considered polyphyletic. A systematic revision of the Actinocrinitidae would require inclusion of the Periechocrinidae and is beyond the scope of this study. We continue to use the present classification for convenience, noting the general morphologic relationships of the taxa described for future reference.

Identification of genera of the Actinocrinitidae is difficult based on fragmentary thecae or calyces in which the tegmen or distal ends of the protruded arm lobes are absent. Fragmentary material commonly does not provide information about the shape of the calyx which is important in the present classification. The presence or absence of an anal tube is recognised as the major difference between *Aacocrinus* and *Diatorocrinus*. Without the distal ends of the protruded arms, it may be impossible to tell the number of arms per ray, which is the major difference between *Actinocrinites* and *Aacocrinus*. In some instances the number and type of free arms may be needed, such as *Cytidocrinus* and *Manillacrinus*.

Subfamily ACTINOCRINITINAE Austin & Austin, 1842
**Actinocrinites** Miller, 1821

TYPE SPECIES. *Actinocrinites triacontadactylus* Miller, 1821 from the Tournaisian Mountain Limestone, England; by subsequent designation of Wachsmuth & Springer, 1881.

REMARKS. *Actinocrinites* is thought to have evolved from a periechocrinid in the Late Devonian or Early Carboniferous (Moore & Laudon, 1943) and was exceedingly abundant in the Tournaisian of North America and Europe declining in the Visean. *Actinocrinites* has also been reported in the Early Carboniferous of Japan (Minato, 1951; Minato et al., 1979), eastern Australia (de Koninck, 1878, 1898; Etheridge, 1892; Pickett, 1960) and northern Africa (Termier & Termier, 1950). Webster & Lane (1987) considered Silurian, Devonian and Permian species (Bassler & Moodey, 1943) to be incorrectly assigned to the genus. They also believed many of the Carboniferous species to be synonyms; there are 61 Carboniferous species currently assigned to the genus (Webster, unpublished data). Ausich & Kammer (1991) placed 4 species in synonomy, while establishing one new species, in a morphometric and qualitative analysis of the late Osagean and Meramecian *Actinocrinites* of the Mississippian stratotype region. Additional studies of this type should help resolve the current taxonomic morass of the genus.

We consider the Australian species of *Actinocrinites* described herein to be new species. They are left in open nomenclature, because some specimens are poorly preserved, unsuitable to serve as holotypes and the taxonomy of *Actinocrinites* must be resolved to allow proper comparisons.

**Actinocrinites polydactylus** Miller, 1821

*Actinocrinus polydactylus* de Koninck, 1878: 160, pl. 6, fig. 3. 1898: 122, pl. 6, fig. 3.

REMARKS. De Koninck (1877, 1898) described an internal mould of a compressed calyx from Glen William as *Actinocrinus polydactylus* (sic). The basal view of the specimen has a pentagonal axillary second primibrach; it lacks the tegmen and the ornamentation is unknown. The generic assignment is questionable because the arms are not grouped and protruded as in *Actinocrinites*.

Because the ornament is not preserved, the specific assignment is doubtful. It is possible that the specimen is immature and belongs with Actinocrinitid indet. described below.

### **Actinocrinites** sp. 1
(Figs 1A-E, 2; Table 1)

MATERIAL. QMF38927-38935 from QML508, late Tournaisian, Malchi Formation. All specimens crushed during burial and plates leached by weathering; description based on latex casts. QMF38927, calyx oriented with basal circlet centred; E and A rays show secundibrachs, B ray shows proximal tertibrachs. QMF38928, distal part of theca, tegmen and anal tube. QMF38929-38933, calyces with proximal tertibrachs. QMF38934, partial calyx, base up. QMF38935, partial calyx, on side. GSQF10866 and 13489 from GSQL K-21, Visean?, Caswell Creek Group.

DESCRIPTION. Calyx medium sized; arms grouped; tegmen highly arched with long slender anal tube; all plates below tegmen inflated, with prominent hexagonal stellate ridge ornament. Basal circlet large, tripartite, horizontal proximally, widely flaring distally; base with large circular stem facet with narrow crenularium on outer margin; base of stellate ridges at horizontal to widely flaring flexure. Radials 5, hexagonal, large, subequal, moderately flared. Primanal large, in radial circlet; distal anals unknown. Primibrachs 2; first primibrach hexagonal, adjoined on each side by 2 interprimibrachs; second primibrach axillary, heptagonal, adjoined laterally by 2 interprimibrachs on each side. Secundibrachs 2-4, normally 2. Tertibrachs biserial and free above 2nd tertibrach. Interbrachial series 1-2-3 or 4 -?. Minimum 6 arms per ray, where free. Intersecundibrachs not common, rarely 1 or series 1-1. Tegmen moderately high, many small to intermediate inflated ambulacral and interambulacral plates; ambulacral plates slightly larger and elevated above interambulacral plates, with rounded to irregular central nodes. Anal tube projecting above tegmen, with distal anal opening, slender, of alternating rectangular and larger hexagonal plates in tiers, with hexagonal plates of one tier interlock above and below with rectangular plates of adjacent tiers; considerable variability in plate size, extra plates inserted to compensate.

Stellate ridges 4 (2 on either side of sutures to adjacent basal, inner 2 merging at centre of radial) or 5 (from centre of each basal plate) extend from basal circlet to radials and anal. 3 or 4 ridges continue onto primibrachs with ray ridge largest; 3 or 4 subhorizontal ridges from radials to adjacent radials or anal, central ridge largest; 3 subhorizontal cross ridges from 1st primibrach to 1st interprimibrach or 2nd anal, central ridge largest; 3 diagonal ridges from radials to 1st interprimibrachs, central ridge largest; subhorizontal and diagonal ridges continue onto 2nd tier of interprimibrachs; lateral ridges merge across plates to form small triangles at apices of plate junctions; triple ridges continue on interprimibrachs to tegmen; single ridge continues on secundibrachs, tertibrachs, and intersecundibrachs; distally ridges grading into discontinuous aligned nodes or decrease in number in some interrays.

Stem circular transversely, heteromorphic; noditaxis N323132313231323. Columnals much shorter than wide; latus convex; lumen large, circular; articulum with narrow crenularium, slightly narrower areola and narrower spatium; nodals may bear short spines between cirral facets.

TABLE 1. *Actinocrinites* sp. 1 measurements (mm). * = incomplete or crushed.

| | 38927 | 38931 | 38928 |
|---|---|---|---|
| Calyx diameter* | 34.5 | | |
| Thecal length (estimated) | 25.0 | 38.0 | |
| Basal circlet diameter | 9.9 | 11.1* | |
| Basal circlet length | 3.6 | 4.0 | |
| Radial length | 6.3 | 10.8 | |
| Radial width | 8.6 | 11.7 | |
| First primibrach length | 5.9 | 8.5 | |
| First primibrach width | 6.6 | 8.4* | |
| Second primibrach length | 3.3 | 6.0 | |
| Second primibrach width | 5.5 | 7.7 | |
| First secundibrach length | 7.5 | | |
| First secundibrach width | 6.6 | | |
| Stem facet diameter | 3.7 | 3.5 | |
| Tegmen length* | | | 15.5 |
| Anal tube length* | | | 15.8 |
| Anal tube diameter | | | 6.3 |

REMARKS. *Actinocrinites* sp. 1 differs from *A.*? sp. 3 by having more complex stellate ornamentation. The ornament of *A.*? sp. 3 consists of inflated ossicles with apical pits and single stellate ridges that are confined to the impressed sutures, not expressed as ridges across the inflated surface. *Actinocrinites* sp. 2 lacks thecal plate ornament except for impressed sutures and apical pits. The 3 species suggest a progression from unridged to complex stellate ornament. This is not an lineage as *A.* sp. 1 and *A.*? sp. 3 occur together in the Rockhampton Group, whereas *A.* sp. 2 occurs in the younger Caswell Creek Group.

Both single and complex stellate ridge ornaments are developed in *Actinocrinites* and Wachsmuth & Springer (1897) included specimens of both

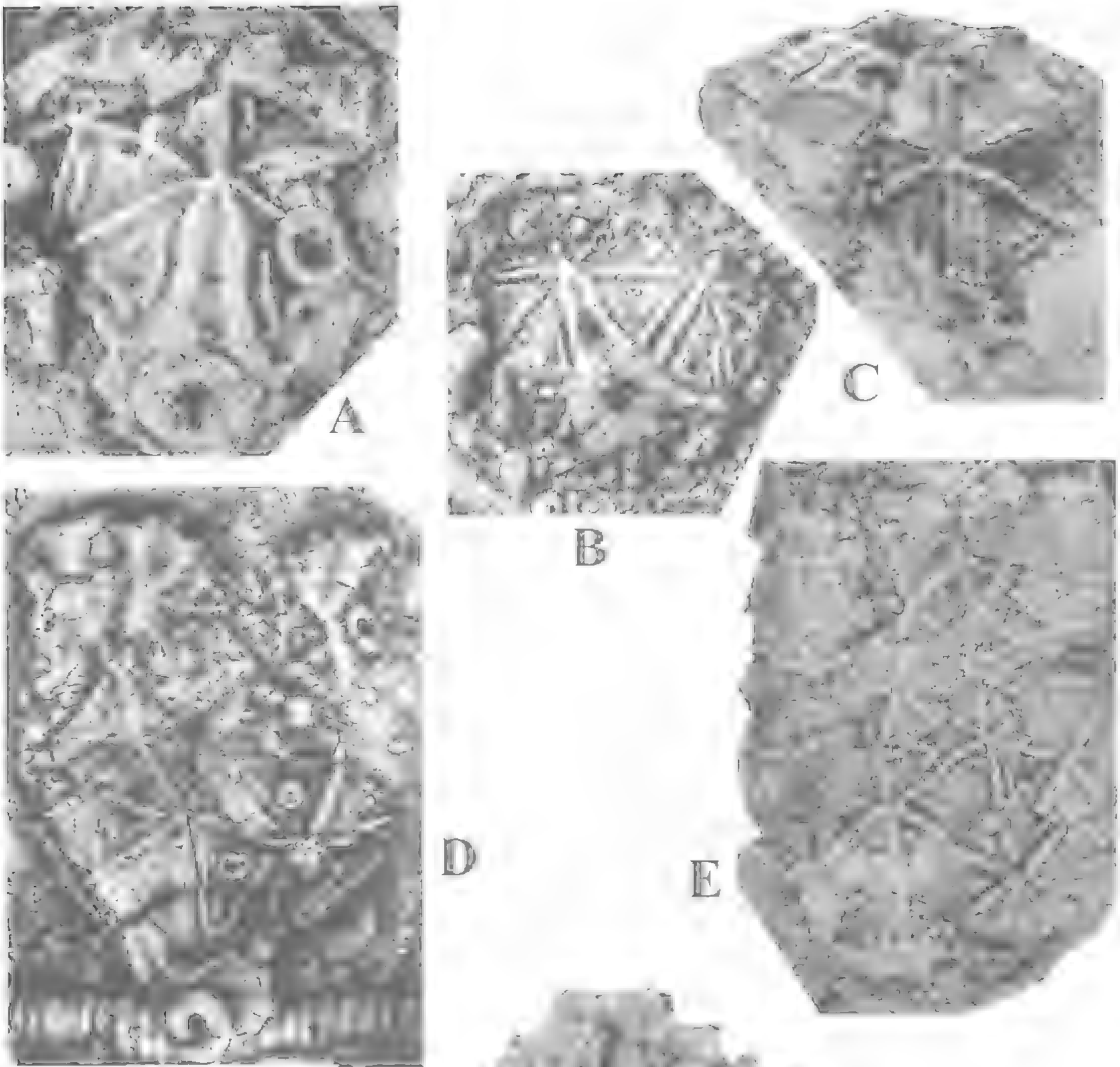


FIG. 2. *Actinocrinites* sp. 1. A, lateral view, ray uncertain, partial calyx QMF38935 ×3.5. B, basal view, rays uncertain, of partial calyx QMF38934 ×2. C, lateral view, ray uncertain, partial calyx GSQF13489 ×2. D, lateral view of partial calyx QMF38929 ×2. E, lateral view of partial calyx QMF38931 ×1.7. F, lateral view, ray uncertain, partial theca GSQF10866 ×2.

types in species such as *A. multiradiatus* (Shumard, 1858) and *A. verrucosus* (Hall, 1858). Single and multiple stellate ridge ornaments are also present in other actinocrinitids and other camerate families. The widespread occurrence and possible repeated development of these features suggest that it is a functional ornament.

Brower (1967) suggested that actinocrinitids may be polyphyletically derived from the periechocrinids, many of which have the single or multiple stellate ridge ornament. The dimerocrinitids are periechocrinoids with infrabasals and should also be considered as possibly ancestral to the actinocrinitids. However, origin of the actinocrinitids is beyond the scope of this study.

A pluricolumnal and disarticulated columnal at the base of the calyx on the slab with QMF38929 are included in *A.* sp.1, as they have the identical articular facet as that of the calyx. A 12.3mm diameter encrusting holdfast with a round articular facet (3.7mm diameter) bearing a central depression and large circular lumen impression is on this same slab and may belong to an immature *Actinocrinites* sp. 1.

This description is based on QMF38927, 38928 and 38931, with variations noted from other specimens.

**Actinocrinites** sp. 2
(Figs 3, 4D)

MATERIAL. GSQF13490-13494 from GSQL3006, early or middle Tournaisian, Neil's Creek Clastics.

DESCRIPTION. Calyx bowl shaped, 20mm long (estimated), 35mm wide (estimated), sutures impressed; calyx plates inflated, without ribbing; arms grouped, flaring with 1st primibrach; tegmen probably moderately inflated with anal tube. Basals 3, equal, horizontal proximally, flared distally, visible in side view of cup; basal circlet diameter 8.4mm. Radials 5, heptagonal, large, 6.9mm long, 7.6mm wide, moderately flaring. Primanal hexagonal, in radial circlet; anal series: P-2-3-3 minimum, continuing onto tegmen. First primibrach hexagonal, 5.4mm long, 5.8mm wide, incurved slightly from radials. Axillary 2nd primibrach heptagonal, adjoined laterally by 2 interray plates, outflaring distally. First secundibrach hexagonal, wider than long, strongly outflaring. Axillary 2nd secundibrach pentagonal, wider than long, gently upflaring. Arms free with first or 2nd tertibrach. Four arms per ray. Interray series: 1-2-3-2-?, extending onto tegmen. Tegmen of many interambulacral plates, 1.7 long, 1.1 wide to 2 long, 2 wide. Numerous ambulacral plates increase in size towards anal tube, 0.6 long, 0.6 wide to 1.8 long, 1.7 wide. Anal tube subcentral. Stem impression circular, 4mm diameter.

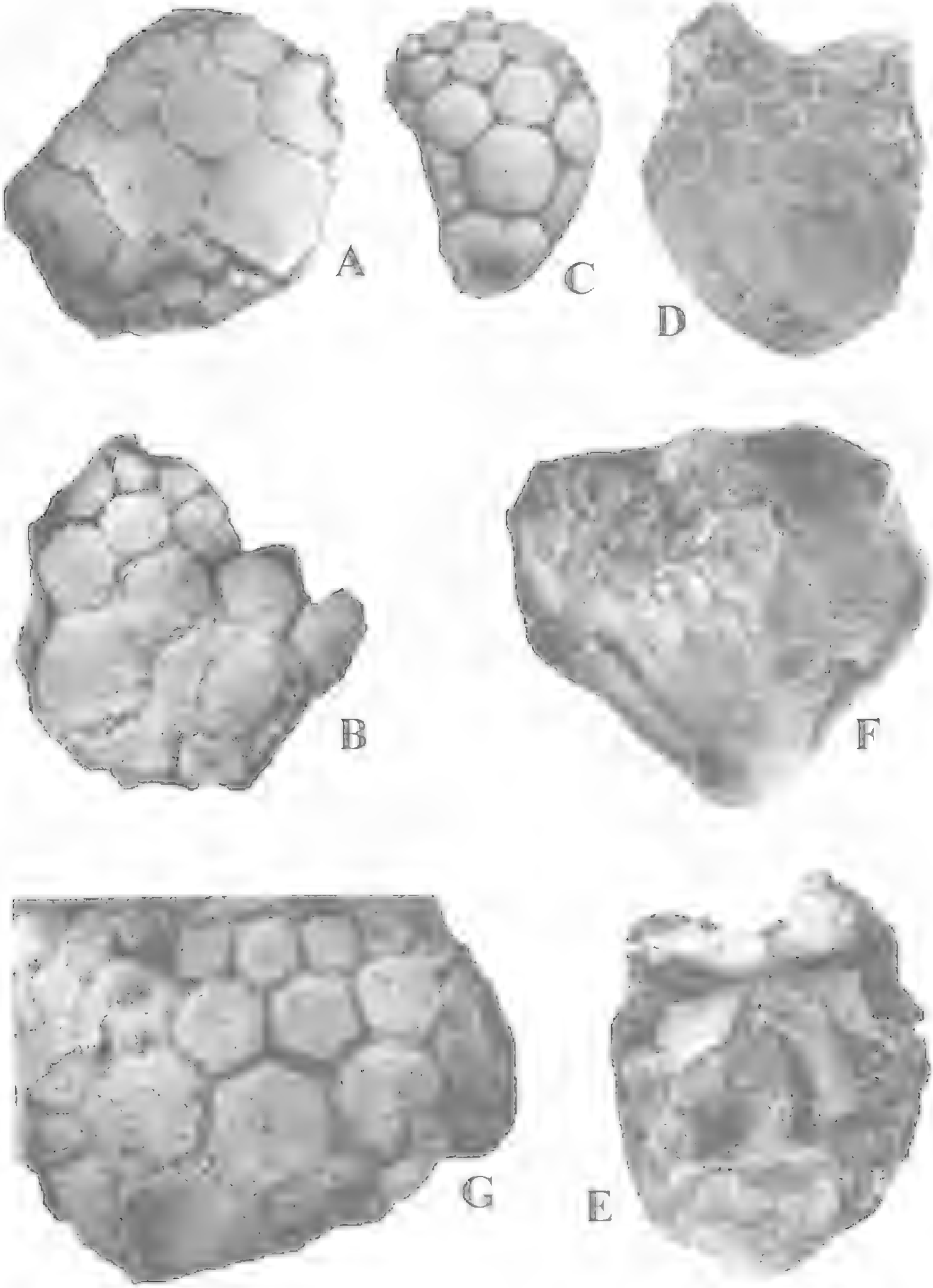
REMARKS. GSQF13490 consists of the internal and partial external moulds of a theca. The internal mould of the calyx is distorted slightly along the D-AB axis, with the tegmen crushed down into the visceral cavity. Ambulacral trackways are elevated above the interambulacral areas, and the proximal part of the slightly eccentric anal tube projects above the ambulacral areas. The tegmen would have been moderately inflated. The external mould preserves the non-stellate character of the inflated plates of the basal circlet, the B ray and adjacent parts of the interrays on either side. GSQF13493 is the external mould of a calyx crushed along the A-CD axis, retaining the basal circlet, radials, primibrachs and parts of the interrays; the anal series is lost. GSQF13492 is an internal mould of a part of the tegmen, showing growth lines on some ossicles. The unnumbered specimen is an external impression of a fragment of 2 rays and the interray from the distal ends of the radials through the 1st secundibrachs. It would have been the largest individual of the 5 specimens as a primibrach is 10.3mm long and 10.9mm wide, nearly twice the dimensions of the primibrach of GSQF13490, the most complete specimen. GSQF13491 is a crushed partial theca and GSQF-13494 the external mould of a partial theca.

**Actinocrinites**? sp. 3
(Fig. 4E,F)

MATERIAL. QMF38936 and 38937, moulds of crushed partial thecae from QML508, late Tournaisian, Malchi Formation.

DESCRIPTION. Calyx high, truncated, conical, arms grouped, plate structure like *Actinocrinites* sp. 1, lacking intersecundibrach plates; interprimibrach series 1-2-3-?. Anal series and tegmen unknown. Minimum 4 arms per ray, inner facet on axillary secundibrach wider than outer. Stem facet circular; lumen circular; articulum narrow, areola more than twice width of articulum, spatium intermediate width.

FIG. 3. *Actinocrinites* sp. 2. A,B, B ray and D-E interray views of partial calyx GSQF13493. C-E, B ray, internal A-B interray and oblique internal tegmen views of GSQF13490. F, lateral view of partial tegmen GSQF13492. G, interray view of partial calyx GSQF13494. All ×2.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QMF38936: Calyx 25.5mm long (estimated); basals 5.2mm long (estimated); radials 6.8mm long, 7.4mm wide; 1st primibrach 5.1mm long, 6.0mm wide; 2nd primibrach 4.6mm long, 5.5mm wide. QMF38937: Basal circlet diameter 11.8mm; basals 4.4mm long; radials 8.0mm long, 10.0mm wide; stem facet 4.5mm in diameter.

REMARKS. The lack of stellate ridge ornament across the inflated calyx plates of *Actinocrinites*? sp. 3 is not an artifact of weathering or abrasion, because the stem facets of the basal circlet and broken proximal columnal of QMF38937 show sharp detail of the culmina and crenellae of the articulum and surfaces of the areola and spatium. The generic assignment is questioned because the tegmen is unknown.

### **Aacocrinus** Bowsher, 1955

TYPE SPECIES. *Aacocrinus nododorsatus* Bowsher, 1955 from the Kinderhookian (Tournaisian) Chouteau Limestone of Missouri; by original designation.

### **Aacocrinus acylus** sp. nov.
(Fig. 4A-C)

ETYMOLOGY. Latin, *acylus*, acorn of the holm-oak; refers to the acorn shape of the calyx.

MATERIAL. HOLOTYPE: QMF38953. PARATYPE: QMF-38954, external moulds of calyces from QML1248, Tournaisian or possibly Visean Tellebang Limestone.

DIAGNOSIS. Calyx small, equidimensional; calyx bowl shaped, with single stellate ridge ornament; arms grouped, protruded, flare with axillary 2nd primibrach; tegmen strongly arched, as long as calyx; slightly eccentric anal tube; arms free with tertibrachs, 4 arms per ray; stem facet circular.

DECRIPTION. Calyx small, equidimensional. Calyx bowl shaped; coarse, single-ridge stellate ornament. Basal circlet large, short, proximally horizontal; large impressed circular stem facet, distally upflared, forming base of walls, visible in lateral view. Radials moderately large, strongly convex longitudinally, moderately convex transversely, forming majority of cup wall. Primanal large, in radial circlet, series unknown; 1st primibrach and 1st interprimibrach subvertical, forming distal part of cup wall. Axillary 2nd primibrach widely flared, lacking stellate ridge ornament; 2nd secundibrach axillary; 4 arms per ray; arms free with tertibrachs. Tegmen strongly arched, as long as calyx, formed of orals, three series of ambulacrals and interambulacrals; all plates nodose, commonly with large blunt nodes. Anal tube narrow, slightly eccentric, formed of medium-sized strongly nodose to blunt spined plates. Free arms and stem unknown.

REMARKS. Silicification of the siltstone to fine grained sandstone external moulds of *Aacocrinus acylus* obliterated cup plate sutures except those of the basal circlet. Sutures of the brachials commencing with the 2nd primibrach and tegmen plates are well preserved. The stellate ridge ornament is rounded, vague, but obvious. QMF38953 is slightly crushed from compaction and oriented on its side, whereas QMF38954 does not appear to be crushed and is oriented obliquely on its side with nearly all of the tegmen covered. Neither specimen shows the anal series. The generic assignment is based on the plate arrangement and shape of the calyx.

*Aacocrinus acylus* belongs to the 20-armed group of the genus and has a bowl-shaped calyx, whereas all other species of the genus have a more conical shape. The tegmen has third-order ambulacrals that Brower (1967) noted as the difference between 10- and 20-armed species. Both *A. tetradactylus* Brower, 1967 and *A. chouteauensis* (Miller, 1892), the other 20-armed species, have longer thecae, shorter tegmens and strongly eccentric anal openings.

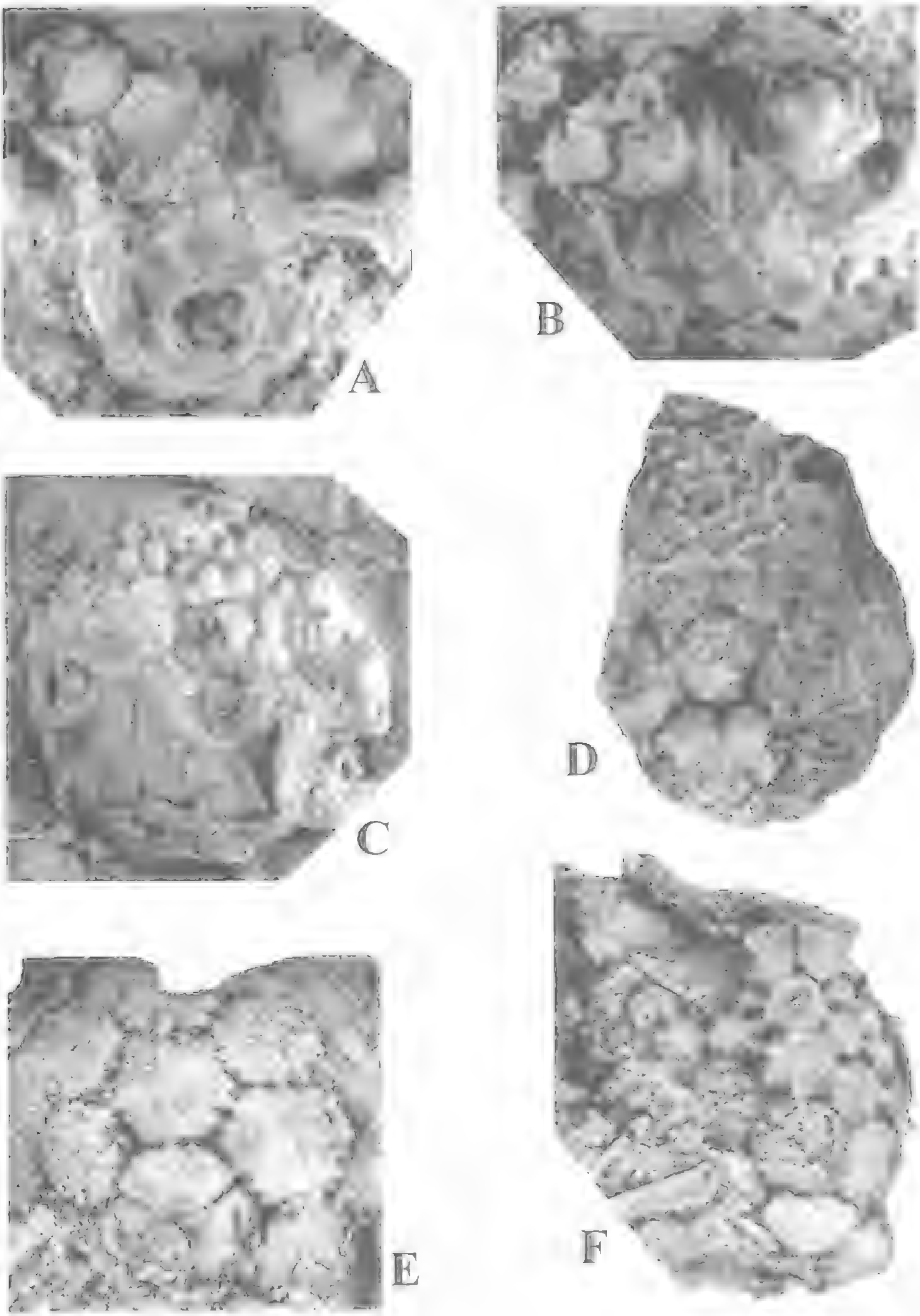
*Aacocrinus acylus* is the first report of the genus outside the United States. Brower (1967) noted that all identified species are from the Kinderhookian of the midcontinent of the United States, but he also recognised an unnamed Osagean form from the same area. Webster & Lane (1987) reported an early Osagean specimen from the Anchor Limestone of southern Nevada.

### **Aacocrinus** sp. 1
(Figs 5A-G, 6B-H)

MATERIAL. QMF38938-38944, latex moulds of crushed partial thecae from QML508, late Tournaisian, Malchi Formation. GSQF10865, 10867, 10868 and 10871a and b, from GSQL K-21, Visean? Caswell Creek Group.

DESCRIPTION. Calyx medium sized; arms grouped; tegmen highly arched with one row of plates forming anal tube; all plates below tegmen inflated with prominent hexagonal single ridge

FIG. 4. A-C, *Aacocrinus acylus* sp. nov., A,B, basal and lateral views of paratype, QMF38954 ×2.6. C, lateral view of holotype theca, QMF38953 ×2.6. D, *Actinocrinites* sp. 2, posterior interray view of GSQF13491 ×1.6. E,F, *Actinocrinites*? sp. 3. E, basal view of partial calyx QMF38936 ×2. F, lateral view of partial theca QMF38937 ×2.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stellate ornament. Basal circlet large, tripartite, horizontal proximally, upflared distally; base with large circular stem facet with narrow crenularium on outer margin; fluting at base stellate ridges at horizontal to upflared flexure. Radials 5, hexagonal, large, subequal dimensions variable, upflared. Primanal large, in radial circlet; distal anals unknown. Primibrachs 2; 1st primibrach hexagonal, adjoined on each side by 2 interprimibrachs; 2nd primibrach axillary, heptagonal, adjoined laterally by 2 interprimibrachs on each side. Secundibrachs 2. Tertibrachs becoming biserial and free after 2nd tertibrach. Interbrachial series 1-2-3-4-tegmen. Tegmen high, formed of many small to intermediate sized inflated ambulacral and interambulacral plates; ambulacral plates slightly larger and with circular to irregular central nodes, elevated above interambulacral plates. Anal opening projecting above tegmen with single row of plates.

Stellate ornamentation of elevated sharp ridges; double and single ridge from basals onto radials and primanal, single ridges on all calyx plates thereafter; double ridge along basal sutures merging at centre of radials to continue as ray ridge; ray ridges largest, subhorizontal and diagonal ridges smaller. Occasional additional accessory node or very short ridge on radials or 1st interprimibrach. Minimum 4 arms per ray, inner facet on axillary secundibrach wider than outer. Stem facet large, circular; lumen large, circular to subpentagonal; articulum narrow, areola more than twice width of articulum, spatium intermediate width.

QMF38938: Calyx 26mm long (est.); basal circlet diameter 10mm, 5.3mm long; radials 7.6mm long, 8.3mm wide; 1st primibrach 6.4mm long, 6.4mm wide; 2nd primibrach 5.7mm long, 6.7mm wide; proximal columnal 5.2mm in diameter.

REMARKS. This description is based on QMF-38938, 38941 and 38942 and GSQF10867. Other specimens are included in this taxon because they have the same type of plate ornament. The single stellate ridge ornament results in a less intricate ridge pattern on the calyx. The wider facets on the inner axillary secundibrachs suggest additional branching of the arms, which would result in 6 arms per ray. Known species of *Aacocrinus* have 2 - 4 arms per ray, whereas most species of *Actinocrinites* have 6 arms per ray and an anal tube of variable length.

*Aacocrinus* sp. 1 differs from *A. acylus* by having a longer, more conical cup and calyx, and a longer tegmen. The tegmen is formed of more numerous plates than any of the American species of the genus and is more similar to that of *Actinocrinites*. *Aacocrinus* sp. 1 is considered a new species but all specimens are incomplete and unsuitable to serve as a holotype.

### **Manillacrinus** Campbell & Bein, 1971

TYPE SPECIES. *Cactocrinus? brownei* Dun & Benson, 1920 from the Namoi Formation, NSW; by original designation.

REMARKS. *Manillacrinus* was incorrectly included in the Eumorphocrininae by Ubaghs (in Moore & Teichert, 1978) and Webster & Lane (1987) as they did not recognise the arm grouping of *M. brownei* (Campbell & Bein, 1971, pl. 50, figs 1, 2, 6, 7) and no mention was made in the original descriptions about the arms grouped and protruded, a character of the Actinocrinitinae. *Manillacrinus* is distinguished from other genera of the Actinocrinitinae by the biserial ramules given off the outer sides of the 2 uniserial arm trunks of each ray.

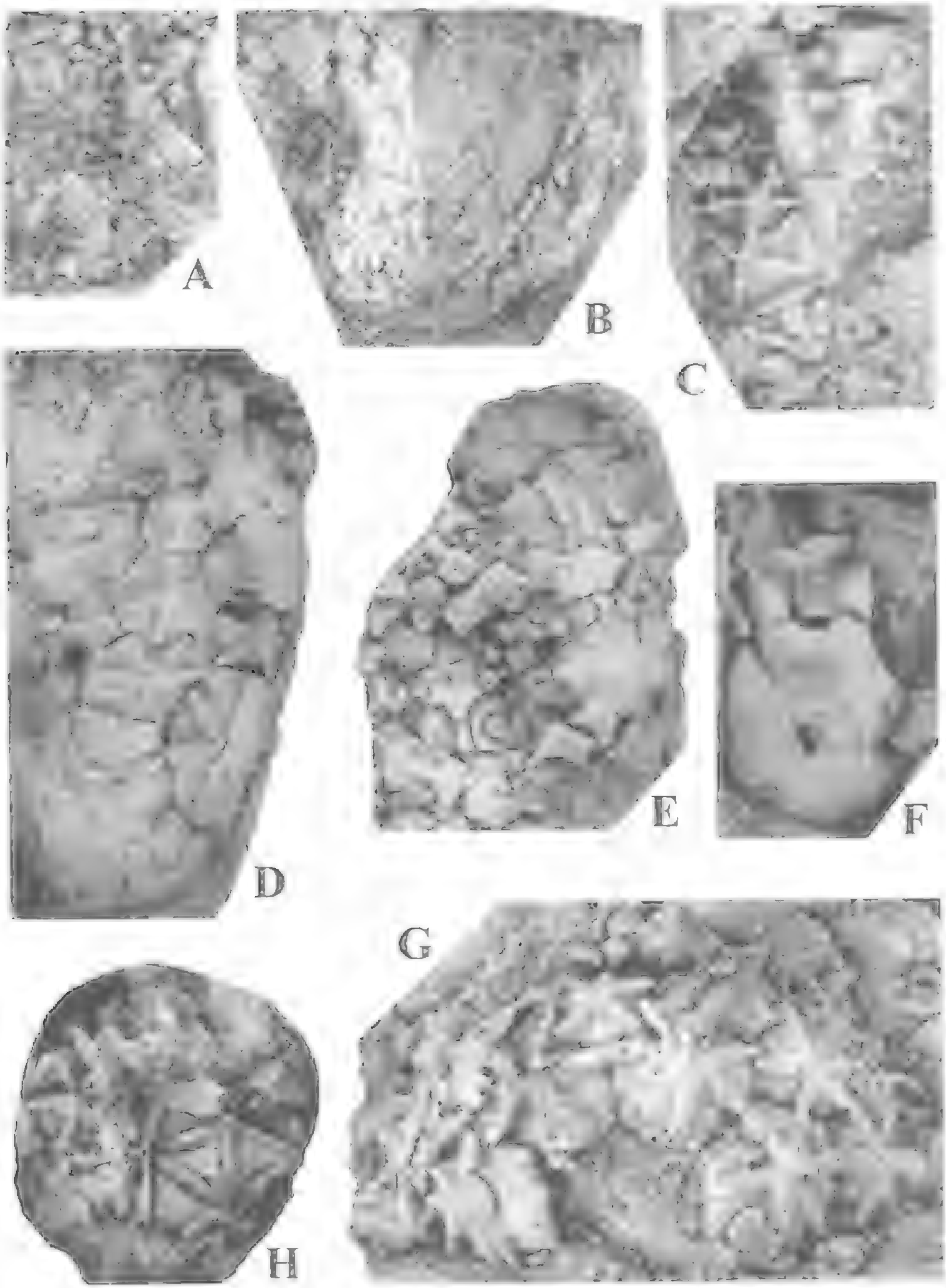
### **Manillacrinus brownei** (Dun & Benson, 1920) (Figs 5H, 6A)

*Cactocrinus? brownei* Dun & Benson, 1920: 342, pl. 19, fig. 1.
*Manillacrinus brownei* (Dun & Benson); Campbell & Bein, 1971: 427, pl. 50, figs 1-7; text-fig. 7.

MATERIAL. QMF38945, an external mould of a partial theca, from QML508, late Tournaisian, Malchi Formation. GSQF13495 from GSQL3012, late Tournaisian Malchi Formation, external mould of partial theca.

REMARKS. *Manillacrinus brownei* has protruded grouped arms; sharply elevated, centrally inflated, single ridge, stellate ornament; and 2 ramule-bearing arms per ray. The 2 ramule-bearing arms, combined with the protruded grouped arms, are the most diagnostic characters of the genus. The single ridge stellate ornament of *M. brownei* is not unique to the genus, but the stellate intersecundibrach plate is not common in actinocrinitids. Also, the stellate ridges continue

FIG. 5. A-G, *Aacocrinus* sp. 1. A, lateral view of partial calyx QMF38939 ×1.7. B, lateral view of partial calyx QMF38938 ×1.6. C, lateral view of partial calyx QMF38943 ×4. D, interray view of partly disarticulated calyx QMF38942 ×2.6. E, view of crushed theca QMF38944 ×2.6. F, view of basal circlet and stem facet QMF38941 ×4.2. G, basal view of partial calyx QMF38940 ×3.6. H, *Manillacrinus brownei* (Dun & Benson, 1920), basal view of partial calyx GSQF13495 ×2.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without significant decrease in development to the base of the tegmen. The partial calyx GSQF13495 is a basal circlet with one ray to the secundibrachs and proximal parts of 2 other rays. It is assigned to *M. brownei* because the stellate ornament is so sharp and the ridges are centrally inflated and highly elevated. It also has the double ridges from the basal circlet to 2 of the radials. The 2nd specimen QMF38945 is the distal part of a calyx with the stellate ridged intersecundibrach in both rays.

**Manillacrinus acanthus** sp. nov.
(Figs 7, 8)

ETYMOLOGY. Greek *acanthos*, spine; referring to the short thorns on some of the ambulacral plates of the tegmen.

MATERIAL. HOLOTYPE: MMF33605. PARATYPES: MMF33431 and 33606; other specimens MMF33435 and AMSF65556, all from the late Tournaisian Namoi Formation, near Barraba, NSW.

DIAGNOSIS. Ambulacral plates with 1 or 2 short blunt spines midway between free arms and anal tube; calyx high conical.

DESCRIPTION. Calyx 62.3mm long; 30.2-50.6mm wide, (40.4mm average), widest at base; tegmen high, conical; plates tumid; apical pits on calyx; multiple stellate ridge ornament to base tegmen; arms grouped, distinctively protruded; tegmen high arched; short central anal tube. Basal circlet tripartite, 9mm long, 12.7mm wide (average), proximally concave, with circular stem facet, distally strongly upflared. Radials 5, septagonal, 12.5mm long, 11.3mm wide, concave to convex longitudinally, moderately convex transversely. Primanal 10.1mm long, 8.6mm wide, gently convex longitudinally, moderately convex transversely, in radial circlet; anal series P-2-3-4-4-tegmen. First primibrach hexagonal, 7.9mm long, 9.0mm wide, moderately convex longitudinally and transversely, adjoined laterally by 2 iIBrr on each side. Axillary 2nd primibrach septagonal, 5.1mm long, 8.2mm wide, straight to slightly concave longitudinally, moderately convex transversely, adjoined on outer side by 2 interprimibrachs. First secundibrach pentagonal, 3.4mm long, 4.8mm wide, longitudinally concave, moderately flaring outward, convex transversely. Axillary 2nd secundibrach pentagonal, 2.5mm long, 5.3mm wide, straight to gently convex longitudinally, convex transversely, widely flaring outward. First and 2nd tertibrachs fixed in calyx, arms free thereafter. Interprimibrach series 1-2-3-2-tegmen; plates convex longitudinally and transversely, decreasing in size distally, last row incurved. Single intersecundibrach octagonal, elongate, with short proximal and distal facets. Multiple stellate ridge ornament of 4-5 ridges from basals to radials, decreasing to single ridge thereafter, continuing to secundibrachs in rays and to tegmen on interbrachs. Tegmen plates large, tumid. Ambulacral plates elevated above interambulacrals, 1 or 2 midway between free arms and anal tube bearing short blunt spines. Anal tube subcentral, formed of 2 rows of polygonal plates. Stem circular; proximal facet 9.5mm diameter (average), with narrow crenularium. Free arms unknown.

REMARKS. *Manillacrinus acanthus* is distinguished from *M. brownei* by the spines on the tegmen and the much more conical theca. The adult specimen is much larger than adult *M. brownei*.

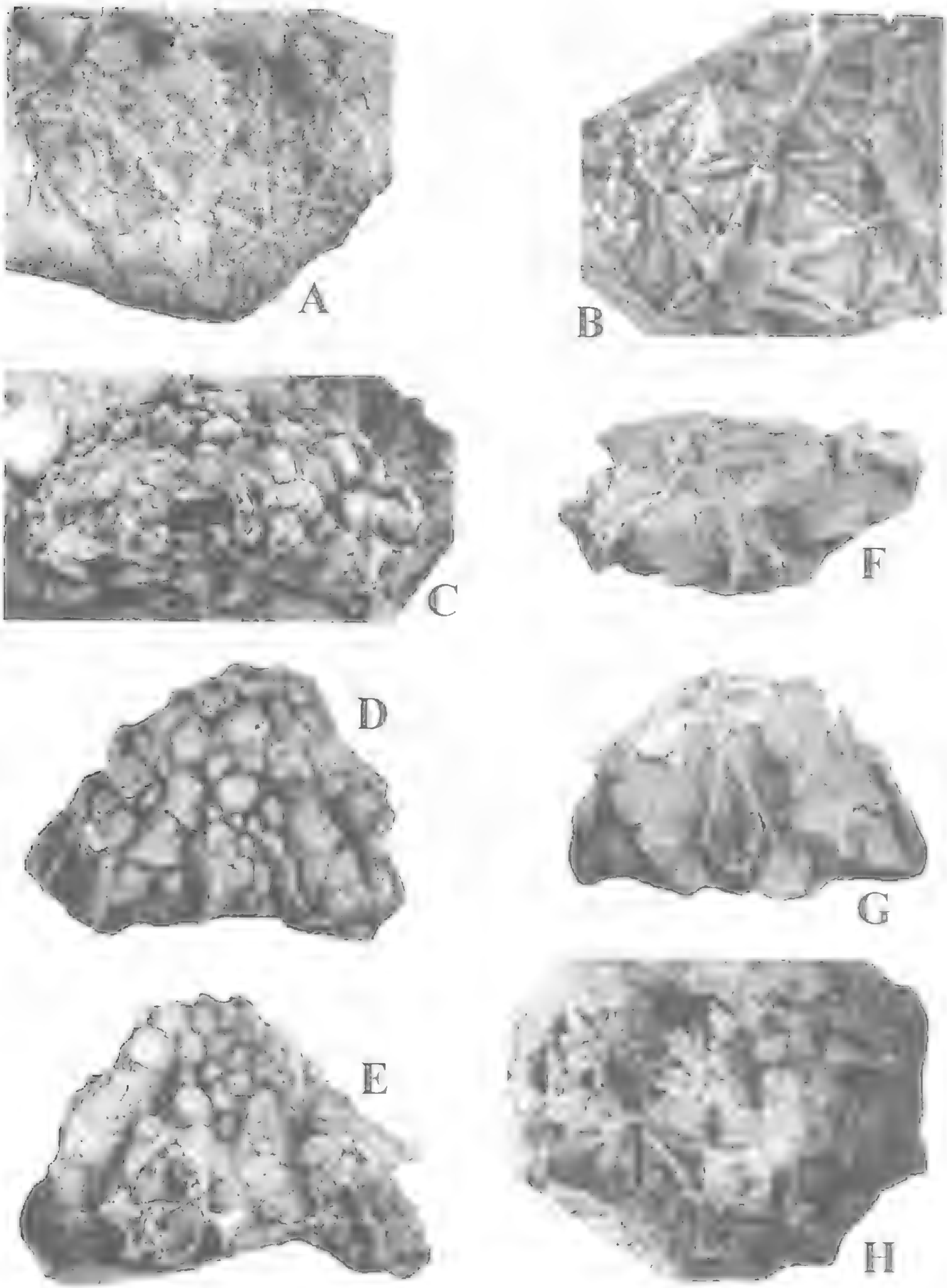
Measurements were taken on the holotype, which is crushed normal to the BC-D plane. Paratype MMF33431 lacks the tegmen. Paratype MMF33606 lacks the basal circlet and the tegmen is crushed into the visceral cavity, but the spines on the ambulacral plates are well-preserved. The stellate ridge ornament is poorly preserved on the types but is recognised best on paratype MMF33431. MMF33435 is abnormal with both the A and B radials followed by 4 primibrachs. The distal parts of the calyx are missing and the distal relationship of the ray and interray plates is unknown. AMSF65556 lacks the basal circlet, but the two radials and next distal plates have well-preserved stellate ridge ornament.

**Sampsonocrinus** Miller & Gurley, 1895

TYPE SPECIES. *Sampsonocrinus hemisphericus* Miller & Gurley, 1895 from the Chouteau Limestone, Missouri; by original designation.

REMARKS. *Sampsonocrinus* is distinguished from *Actinocrinites* by having a lower, more bowl-shaped cup, relatively larger basals and radials and only 4 arms per ray. *Sampsonocrinus* is a

FIG. 6. A, *Manillacrinus brownei* (Dun & Benson, 1920), lateral view of partial calyx QMF38945 ×1.8. B-H, *Aacocrinus* sp. 1. B, lateral view of base of partial calyx GSQF10871b ×2. C-G, B ray, oral, posterior views of tegmen, interior B ray and summit oblique of interior of tegmen of GSQF10867 ×2. H, lateral view of partial theca GSQF10868 ×2.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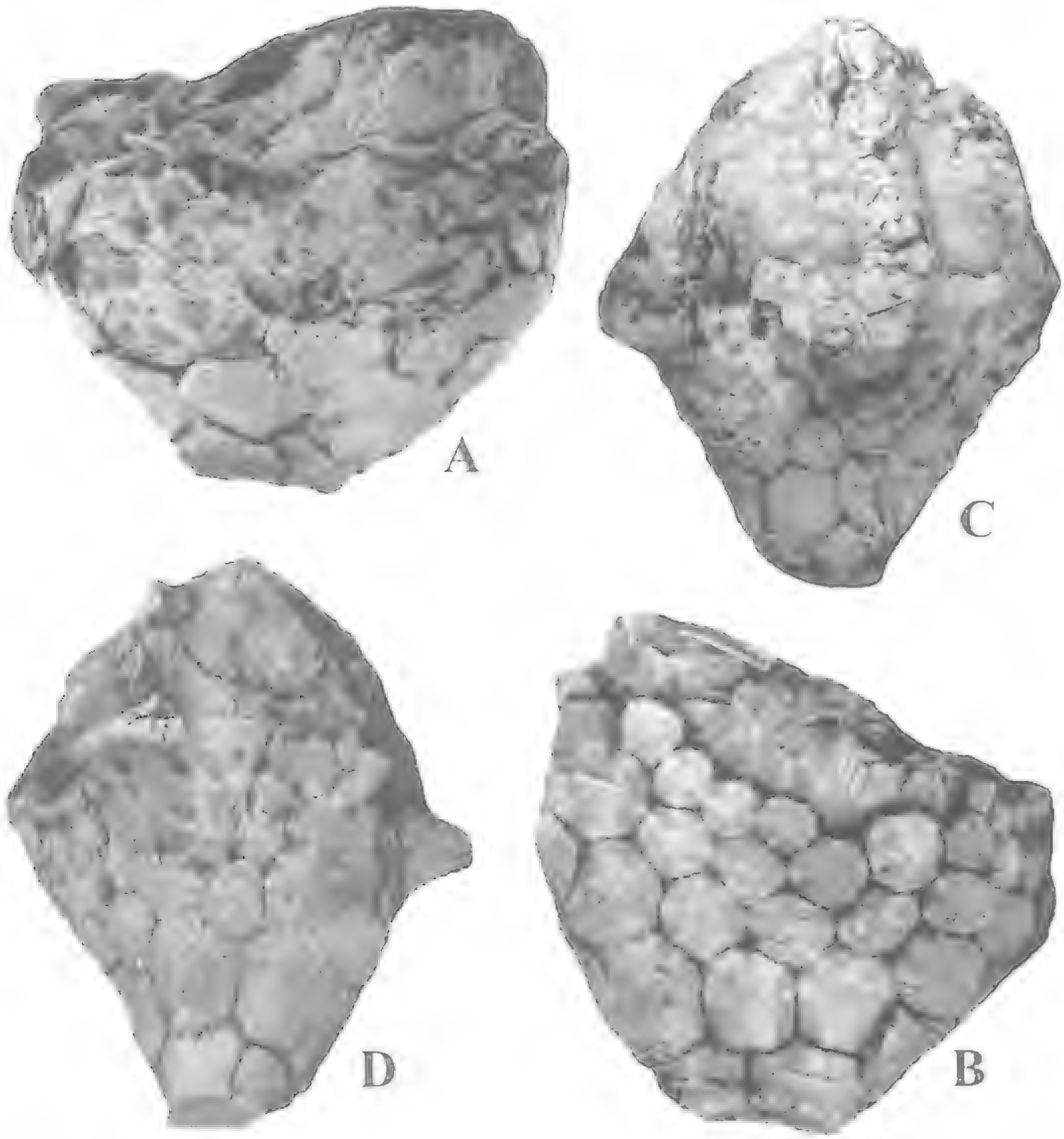


FIG. 7. *Manillacrinus acanthus* sp. nov. A,B, A-E interray and posterior views of paratype MMF33431, lacking tegmen ×1.7. C,D, C ray and A ray views of holotype MMF33605 ×1.2.

Tournaisian genus, previously reported from the United States. United Kingdom records are now excluded from the genus (George Sevastopulo pers. comm.) This is the first report of the genus in Australia.

**Sampsonocrinus cannindahensis** sp. nov.
(Fig. 9)

ETYMOLOGY. From Old Cannindah.

MATERIAL. HOLOTYPE: GSQF10864, external and internal mould of calyx from GSQL K-21, Visean? Caswell Creek Group. PARATYPE: QMF17784, internal mould of cup. Collected by C. W. De Vis (no. 649).

DIAGNOSIS. Cup low, broad, with blunt spines or coarse nodes on each of the tegmen plates.

DESCRIPTION. Calyx low bowl-shaped, 19.6mm long (incomplete), 39.8mm wide; plates inflated, bulbous; sharp simple stellate ridge ornament continuous across sutures on all adjacent plates below tegmen; tegmen moderately inflated; arms grouped, projecting subhorizontally. Basal circlet 4.0mm long (estimated), 8.2mm diameter

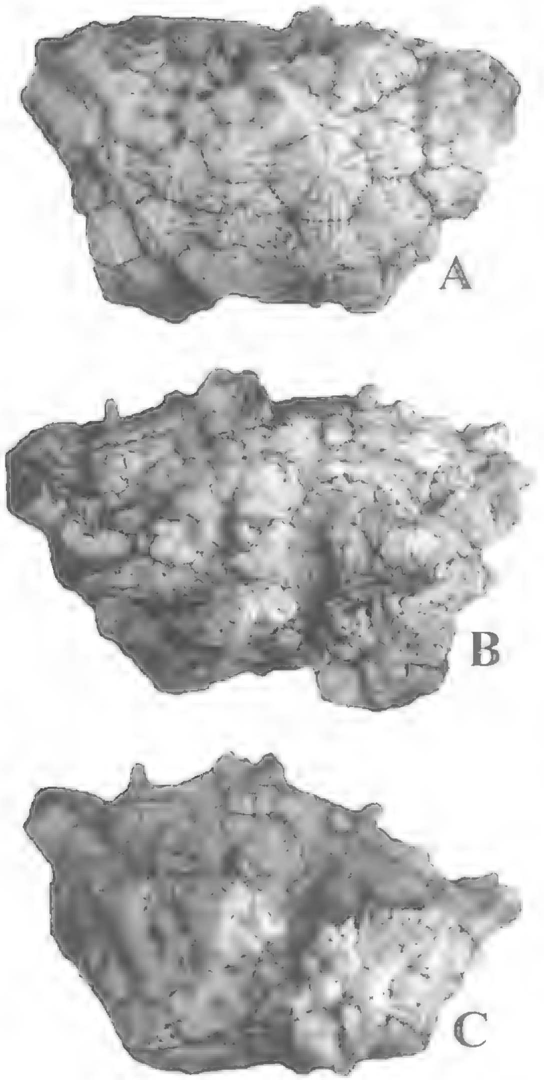


FIG. 8. *Manillacrinus acanthus* sp. nov., A-C, A ray ×1.2), oblique oral ×1.5) and posterior ×1.5) views of paratype MMF33606, lacking basal circlet and tegmen crushed into the visceral cavity.

(internally). Radials 5, hexagonal, 4.8mm long (internal), 7.3mm wide (internal), gently convex longitudinally and transversely, widely outflared. Primanal heptagonal, large, in line with radials; anal series P-2-3-3-2-tegmen, wide. First interradial hexagonal, 5.7mm wide; series 1-2-3-2-tegmen. First primibrach pentagonal, 4.1mm long, 5.4mm wide. C ray 2nd primibrach axillary, pentagonal, 3.0mm long, 3.6mm wide, with distal tip curving outward toward subhorizontal. Single secundibrach axillary, slightly upflared. Arms free with 2nd tertibrach, 4 arms per ray, 20 arms if branching uniform. Tegmen plates relatively small, strongly inflated into short blunt spines. Orals 5, off centre toward anal interray, larger than other tegmen plates, surrounding anal opening at tegmen apex. No anal tube. Ambulacral plates inflated more than interambulacrals with short blunt spines. Stem and free arms unknown.

REMARKS. The holotype internal mould is slightly distorted along the D-AB axis; weathering destroyed most of the external mould of the cup. Ambulacral grooves were elevated above the interambulacral areas, distally merging with them toward the centre of the tegmen, and the eccentric anal tube projected above the tegmen surface. The short calyx of the paratype is crushed inward concentrically around the basal circlet and the tegmen is not exposed.

**Dialutocrinus** Wright, 1955

TYPE SPECIES. *Dialutocrinus milleri* Wright, 1955 from the Tournaisian of England; by original designation.

**Dialutocrinus**? sp.
(Fig. 10A-C)

MATERIAL. QMF33864, a partial calyx, from the Visean? Caswell Creek Group, 7.1 km NE of Monto, on hill on side of road; 24°51'6"S, 151°91'54"E. Collected by Paul Tierney.

DESCRIPTION. Calyx 19.1mm long, 36.3mm wide, conical, with concave sides, with single ridge stellate ornament. Arms very weakly grouped, slightly portruded. Basal circlet 2.5mm long, 11.1mm wide, flat proximally, widely flaring distally, circular stem impression in basal impression. Radials 5, 7.2mm long and wide, heptagonal, moderately bulbous. Primanal smaller than radials, 6.5mm long, 5.5mm wide, moderately bulbous. Anal series P:2:3:4:?, connected with tegmen. First primibrach hexagonal, 3.9mm long, 6.0mm wide, bulbous, slightly concave longitudinally. Axillary 2nd primibrach heptagonal, 3.8mm long, 6.2mm wide, slightly convex longitudinally and transversely. Interprimibrach series 1:2:3:4:3:?, plates decrease in size distally, forming moderately wide gap between arms at rim of calyx. First secundibrach hexagonal, 3.1mm long, 4.7mm wide, weakly flaring. Axillary 2nd secundibrach pentagonal, 2.8mm long, 4.4mm wide, weakly flaring. Intersecundibrach series 1:1. Minimum 2 tertibrachs. Arms not free until 3rd tertibrach or 1st quartibrach. Probably 8 arms per ray. Stem circular transversely, 4.3mm diameter proximally.

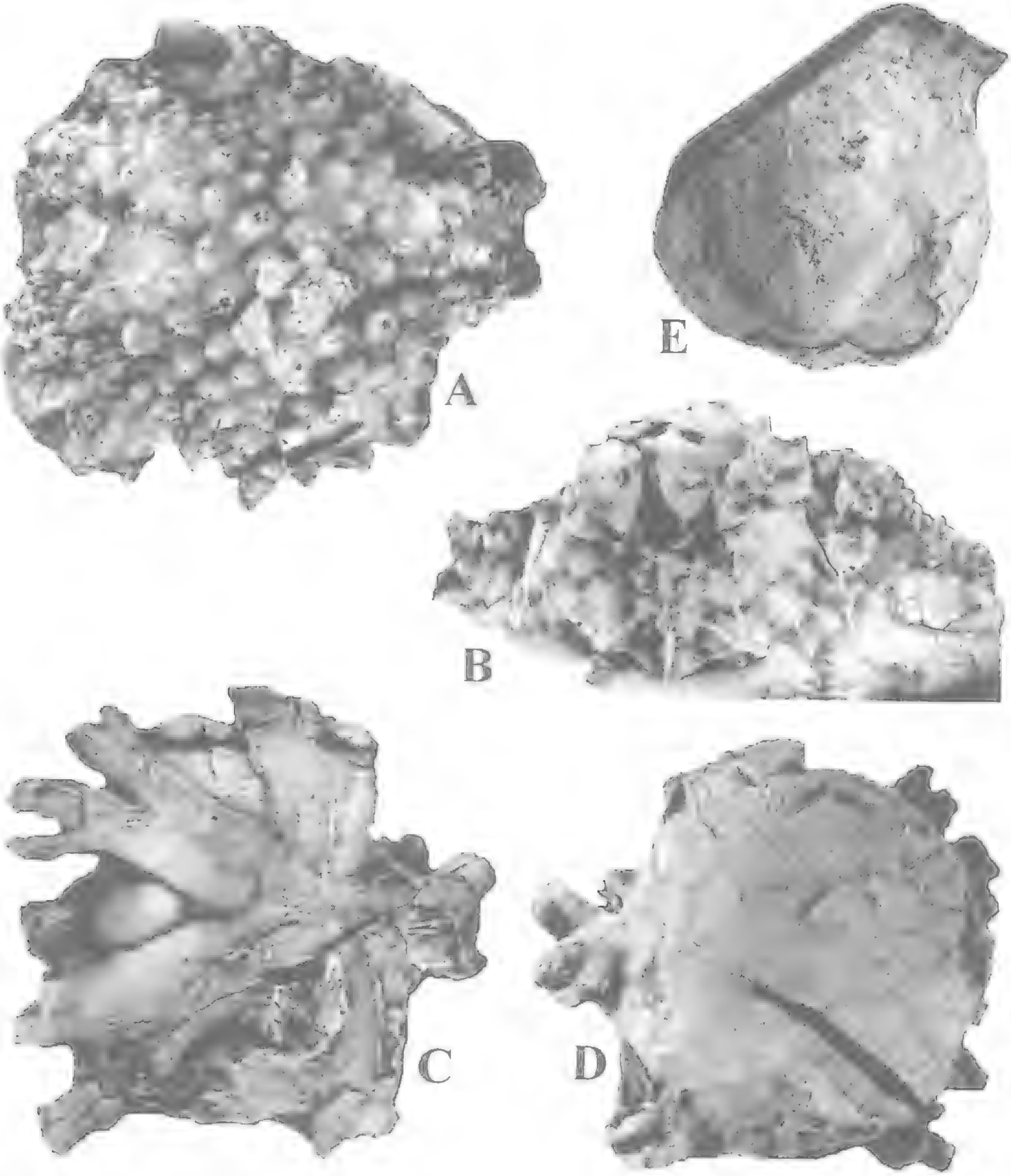



FIG. 9. *Sampsonocrinus cannindahensis* sp. nov., A-D, external oral and E, ray views and oral and basal views of internal mould of holotype, GSQF10864 ×2. F, B-C interray view of internal mould of paratype, QMF17784 ×1.6.

REMARKS. The specimen lacks the tegmen and free arms, and has been slightly distorted by compaction of the cup into the fixed brachials. Plates are recrystallised and the stellate ornament is nearly lost except on the lower 2 rows of plates in the DE interray and adjacent parts of the D and E rays. The specimen is questionably assigned to *Dialutocrinus* because it has 2 secundibrachs and the free arms are unknown. The type species, *D. milleri* Wright, 1955, has a single secundibrach

and the inner arm branches repeatedly above the axillary secundibrach; the outer arm remains unbranched. The wide interprimibrach series (1-2-3-4-3-?), single intersecundibrach, calyx shape, cup plate structure, and ornamentation of *D.*? sp. agrees with *D. milleri*. The specimen may represent a geographical variant.

### **Actinocrinitid** indet.
(Fig. 10D,E)

*Actinocrinus* sp. ind. Etheridge, 1892: 77, pl. 20, figs 6, 7.
?*Periechocrinus indicator* Etheridge, 1892: 78, pl. 22, fig. 4.
?*Periechocrinus*? sp. ind. Etheridge, 1892: 79, text-fig. 1.

MATERIAL. AMSF27094 and 28389 (part and counterpart), locality uncertain within the Clarencetown area. UQF13204, from the Tournaisian Wootton Beds, 3.25 miles N of Clarencetown, on Glen William Rd, NSW.

DESCRIPTION. Calyx 65.5mm long, 56mm wide (incomplete, crushed). Basal circlet tripartite, 23.3mm diameter (minimal), widely flaring. Radials large, 21.3mm long, 21.0mm wide, hexagonal, gently convex longitudinally and transversely, upflared. First primibrach hexagonal, 16.8mm long, 17.4mm wide, gently convex longitudinally and transversely, upflared. Axillary 2nd primibrach pentagonal, 12.7mm long, 15.5mm wide (estimated), concave longitudinally and transversely. Second secundibrach hexagonal, 5.6mm long, 10.2mm wide. Interprimibrach series 1-2-3-?. Anal series, tegmen and stem unknown.

REMARKS. Both specimens are crushed thecae. Measurements were made on AMSF28389. The plates show 9 major growth rings and are preserved as very thin interior rinds. Edges of the plates are preserved as elevated walls marking the sutures. No ornamentation is preserved as the exteriors were lost by weathering. Plates of UQF13204, are weathered and leached, with the remaining calcite very soft and chalky, showing 8 major growth rings.

Provenance of the calyx is given as Clarencetown, NSW. There are numerous lenses of limestone within the Wootton Beds between Clarencetown and Dungog (Lishmund et al., 1985). Both specimens probably derive from this area.

*Actinocrinus* sp. ind. of Etheridge (1892) is probably from the same locality as the described material, or the same horizon from a nearby locality; preservation is similar. Etheridge (1892) reported specimens from the Carboniferous Mirari Limestone, at Greenhills, Paterson to Dungog Road.

*Periechocrinus indicator*, from Carboniferous deposits at Chalky Gully, and *Periechocrinus*? sp. ind., from the Carboniferous Mirari Limestone at Greenhills, described by Etheridge (1892, p. 69-71, pl. 22, fig. 4; text-fig. 1) may also be conspecific with the material described. Neither of the *Periechocrinus* specimens are quite as large, but they have similar plate structure. Also, the former is preserved in the same manner as AMSF28389. If all of these specimens are conspecific, the specific name *indicator* will have priority if a genus is specified.

## Family DICHOCRINIDAE S. A. Miller, 1889
## Subfamily DICHOCRININAE S.A. Miller, 1889

### **Dichocrinus** Munster, 1839

TYPE SPECIES. *Dichocrinus radiatus* Münster, 1839 from the Early Carboniferous of Germany; by monotype.

### **Dichocrinus** cf. **D. laudoni** Broadhead, 1981
(Fig. 11)

MATERIAL. QMF38957, locality and horizon in NSW unknown, probably late Tournaisian Namoi Formation. Collected by G. M. Philip.

DESCRIPTION. Crown small, 12.6mm long (incomplete), 6.0mm wide, expanding gently upward. Cup steeply conical, 7.2mm long, 5.1mm wide, smooth, unornamented. Basal circlet bipartite, steeply upflared, visible in side view, 4.2mm long, 2.6mm wide. Radials 5, longer (4.2mm) than wide (2.6mm), expanded gently distally. Radial facet angustary, projecting slightly above shoulders of radial. Anal not exposed. Brachials strongly convex transversely, straight longitudinally, rectilinear. Second primibrach axillary, isotomous branching, no distal branching on preserved secundibrachs; 10 uniserial arms if branching same in all rays. Stem heteromorphic proximally (noditaxis pattern N1), homeomorphic distally. Columnals circular transversely, diameter 1.5mm proximally; latus gently to moderately convex.

REMARKS. This small crown is flattened in the anterior-posterior plane of symmetry. Brachials at the base of the arms are slightly disarticulated from the radials. The conical cup with the basals making up half the cup wall, 10 arms and uniserial proximal brachials are all primitive features in *Dichocrinus*. The specimen is similar to *D. laudoni*, but the stem does not taper away from the cup as it does on the holotype of *D. laudoni* (Broadhead, 1981, pl. 2, fig. 8). Taper of the stem may be a variable feature as the paratype (Broadhead, 1981, pl. 2, fig. 6) and other specimens (Webster, 1997, pl. 2, figs 5, 10) do not show as strong a taper. Distally, the brachials of

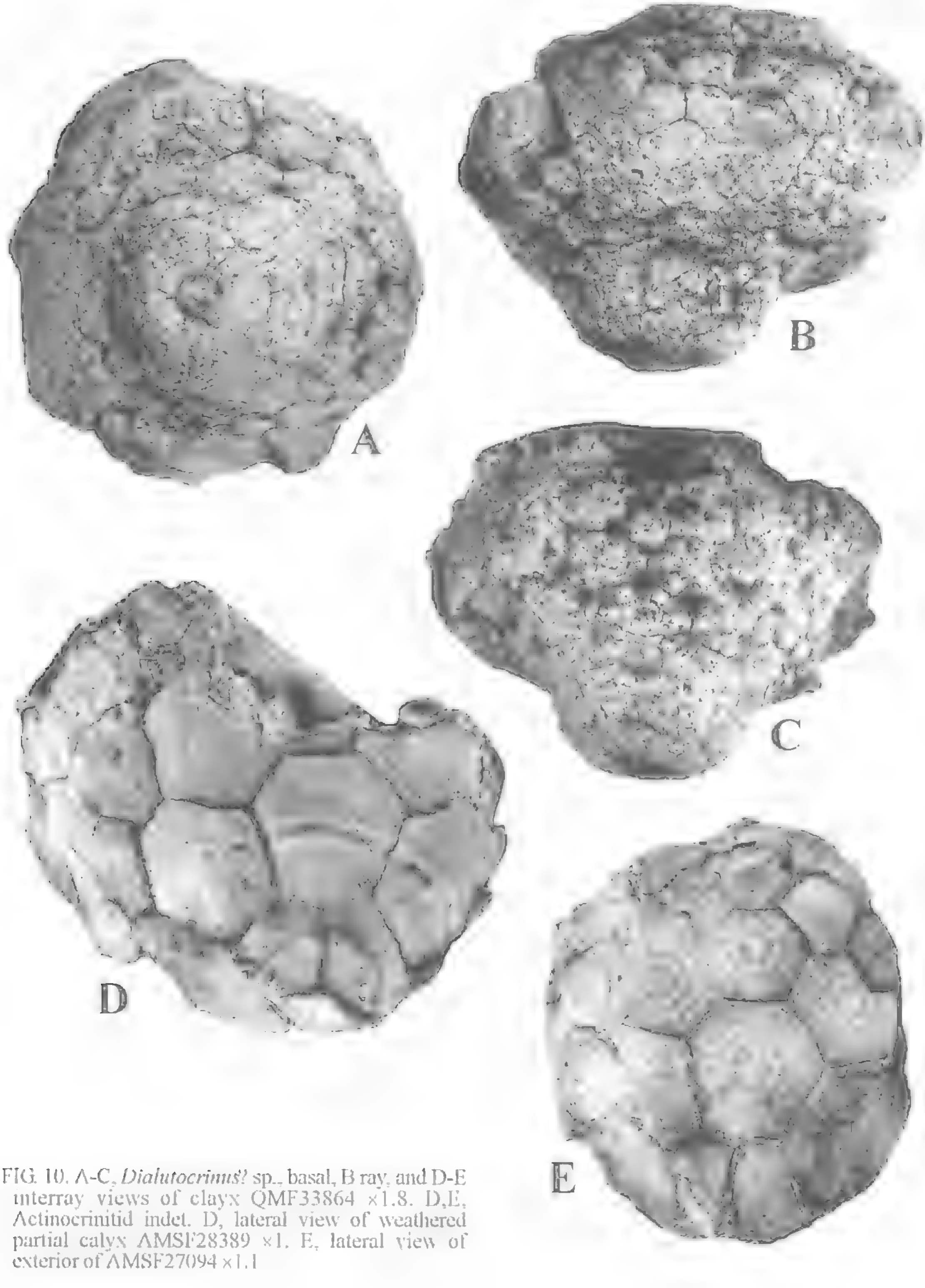



FIG. 10. A-C, *Dialutocrinus*? sp., basal, B ray, and D-E interray views of clayx QMF33864 ×1.8. D,E, Actinocrinitid indet. D, lateral view of weathered partial calyx AMSF28389 ×1. E, lateral view of exterior of AMSF27094 ×1.1

FIG. 11. *Dichocrinus* cf. *D. laudoni* Broadhead, 1981, lateral view of upright crown QMF38957, with Scytalocrinid? indet., lateral view of horizontal crown QMF38958 ×3.

*D. laudoni* become cuneate, whereas the distal brachials of *D.* cf. *D. laudoni* are unknown. They probably become cuneate as this is a feature common to all uniserial species of the genus. If new material is found to show that the brachials do not become cuneate distally, this Australian specimen could represent a new species. In *Dichocrinus* only *D. cintus* Miller & Gurley, 1890 and *D. fusiformis* Austin & Austin, 1844 have 10 arms, but both have surface ornament on the cup plates. All 3 of the 10-armed species of *Dichocrinus* are of middle or late Tournaisian age, suggesting a similar age for *D.* cf. *D. laudoni*.

The specimen is on a small slab associated with an indeterminate scytalocrinid? and a rhodocrinitid.

Family ACROCRINIDAE Wachsmuth & Springer, 1885
Subfamily GLOBACROCRININAE
Moore & Strimple, 1969

**Denarioacrocrinus** gen. nov.

TYPE SPECIES. *Denarioacrocrinus neerkolensis* gen. et sp. nov. from the late Namurian or early Westphalian part of the Neerkol Formation, near Stanwell, Queensland.

ETYMOLOGY. Latin *denarius*, containing 10; refers to the 10 distal intercalaries.

DIAGNOSIS. Calyx vase-shaped; basal circlet unknown; strongly rounded, angustary radial facets, sloping downward outward; minimum 5 rows of intercalaries; 10 plates in distal row, 1 in line with single anal, 3 in line with A, D and E radials, all others interradial; 4 arms per ray.

REMARKS. Moore & Strimple (1969) noted the explosive evolution in the acrocrinids in the Middle to Late Carboniferous of the midcontinent region of the United States. The Globacrocrininae retains the narrow radial facets and advanced genera have a flat basal circlet not visible in lateral view. Genera are defined mainly on the number of distal intercalaries. *Denarioacrocrinus*, with 10 distal intercalaries, is intermediate between the Morrowan to Desmoinesian *Globacrocrinus*, with 8, and the Missourian *Cauacrocrinus*, with 11 distal intercalaries. *Denarioacrocrinus* is the first Late Carboniferous globacrocrinid with part of the arms preserved. The 4 arms per ray are an advanced condition compared to the Early Carboniferous *Protacrocrinus* with 2 and *Springeracrocrinus* with 3.

**Denarioacrocrinus neerkolensis** sp. nov.
(Fig. 12A-C)

ETYMOLOGY. From the Neerkol Formation.

MATERIAL. HOLOTYPE: GSQF10875a and b, internal and external thecal moulds from GSQLK106, late Namurian or early Westphalian, Neerkol Formation.

DIAGNOSIS. As for genus.

DESCRIPTION. Calyx vase-shaped, 22.9mm long (incomplete), 16.5mm wide (slightly crushed), widest at midlength, suture flush, fine vermiform ornament. Basal circlet not preserved. Intercalaries mostly hexagonal, moderately large, minimum 5 rows. Distal row of intercalaries 10 plates, 3 in line with radials (A, D and E), 1 under anal, all others interradial. Distal intercalary next to anal series below C radial, 5.1mm long, 5.1mm wide (estimated), gently convex, subvertical. A and D

radials hexagonal, proximally adjoining 3 intercalaries; C and E radials pentagonal, proximally adjoining 2 intercalaries; E radial pentagonal with proximal tip adjoining distal tip of in line intercalary; all radials gently convex transversely, straight to slightly convex longitudinally, subvertical. C radial 4.7mm long, 6.3mm wide. Radial facet angustary, sloping downward outward, strongly convex externally, below radial summit, with transverse ridge. Anal plate large, hexagonal, 5.5mm long, 4.5mm wide, distal half in line with radials. Tegmen formed of small plates, projecting above radial summit. Arms slender, isotomously branching on 2nd primibrachs and 2nd secundibrachs, 4 per ray, 20 arms if all rays branch as C ray. Proximal brachials cuneate, convex longitudinally, strongly rounded transversely, horseshoe-shaped, with pinnule on long side. Distal brachials unknown, probably biserial.

REMARKS. This calyx is slightly distorted from compaction and lacks the basal circlet. The vase-shape, multiple rows of intercalaries and angustary radial facets are primitive features of the Globacrocrininae, whereas 4 arms per ray is an advanced feature. This was the first crinoid reported (McKellar, 1966) from the Late Carboniferous of Australia.

**Denarioacrocrinus? ornatus** sp. nov.
(Fig. 12D-F; Table 2)

ETYMOLOGY. Latin *ornamentus*, ornament; referring to the stellate and granulate ornamention.

MATERIAL. HOLOTYPE: GSQF10877a and b from GSQL334. PARATYPE: GSQF10876 from GSQLK106, late Namurian or early Westphalian Neerkol Formation.

DIAGNOSIS. Alternating 6 rectangular and 6 hexagonal first row of intercalaries above the basals and stellate ornament on cup plates; sutures impressed.

DESCRIPTION. Calyx vase-shaped, widest at midlength. Bipartite basals horizontal, in basal impression, followed by 7 rows of intercalaries increasing in size distally. Sutures impressed. Plates mostly hexagonal after first row of alternating 6 rectangular and 6 hexagonal plates. Rows staggered with plates interlocking distally and proximally. Occasional pentagonal or heptagonal plate where interlocking adjusted for smaller plate. Plates with stellate ridge ornament radiating from centre of plate to all adjacent plates. Longitudinal ridge developed most strongly on basal row of intercalaries. Fine nodose to vermiform ornament, nodes may be aligned to stellate ridges or sides of plates. First row of intercalaries horizontal, rectangular ossicles strongly convex longitudinally. hexagonal ossicles forming base of calyx; hexagonal plates distal tips visible in lateral view. All following intercalaries subvertical. Stem circular transversely; columnals with wide aureola, narrow crenularium, small ?pentagonal lumen.

REMARKS. GSQF10877a and b are the internal and external moulds of the base of one partial calyx up to the 3rd row of intercalaries. GSQF-10876 is a partial calyx lacking the radials and tegmen. It is crushed along the anterior-posterior plane of symmetry.

*D.? ornatus* is distinguished from *D. neerkolensis* by the stellate ornament and plate arrangement of the 1st row of intercalaries. This is the 1st acrocrinid known with stellate ornamentation. Lacking the radials and complete row of distal intercalaries generic assignment must be questioned.

Suborder GLYPTOCRININA Moore, 1952
Superfamily PLATYCRINITOIDEA
Austin & Austin, 1842
Family PLATYCRINITIDAE
Austin & Austin, 1842

**Platycrinites** J.S. Miller, 1821

TYPE SPECIES. *Platycrinites laevis* Miller, 1821 from the Early Carboniferous of England; by subsequent designation of Meek & Worthen, 1865.

**Platycrinites nux**?
(Etheridge, 1892) nomen correctum
(Fig. 14I,J)

MATERIAL. GSQF10870, an internal mould from GSQLK-21, Visean? Caswell Creek Group.

REMARKS. An internal mould of a cup, designated *Platycrinus*? *nux* by Etheridge (in Jack & Etheridge, 1892) and mentioned by Etheridge

TABLE 2. *Denarioacrocrinus*? *ornatus* sp. nov. measurements (mm).

| | F10877 | F10876 |
|---|---|---|
| Calyx length | | 24.2 |
| Calyx width | | 15.6 |
| Diameter basal circlet (maximum) | 6.9 | |
| Diameter basal circlet (minimum) | 5.9 | |
| Intercalary 1 rectangular, length | 1 | |
| Intercalary 1 rectangular, width | | |
| Intercalary 1 hexagonal, length | | |
| Intercalary 1 hexagonal, width | | |
| Diameter stem impression | 3.4 | 5.6 |

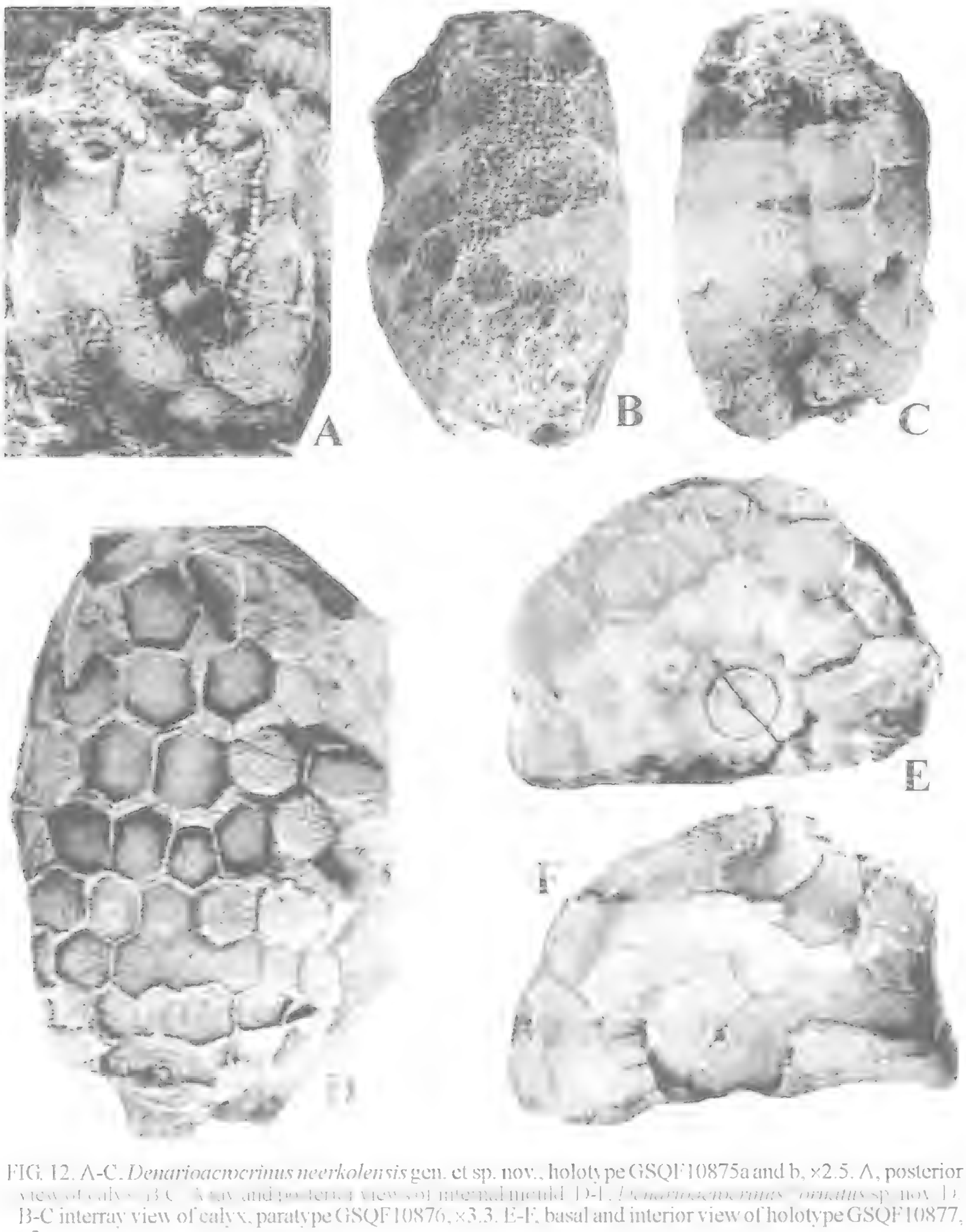



FIG. 12. A-C. *Denarioacrocrinus neerkolensis* gen. et sp. nov., holotype GSQF10875a and b, ×2.5. A, posterior view of calyx. B-C, A ray and posterior views of internal mould. D-F, *Denarioacrocrinus? ornatus* sp. nov. D, B-C interray view of calyx, paratype GSQF10876, ×3.3. E-F, basal and interior view of holotype GSQF10877, ×3.

(1892) has a high bowl-shaped basal circlet and vertical elongate radials. An internal mould (GSQF10870) of a cup from the Early Carboniferous Caswell Creek Group, near Old Cannindah is nearly the same size and has the same shape and plate [illegible]

of these specimens in size and proportions, as well as the type of preservation, suggests that they are from the same stratigraphic unit. Etheridge (in Jack & Etheridge, 1892) reported the specimen from the Middle or Marine Series of the Bowen river Coal Field, 21°20'S, 148°30'E; this is in the Lizzie Creek Volcanics. We wonder if, for unknown reasons, the locality information given by Etheridge (in Jack & Etheridge,1892) could be incorrect or if the specimen was reworked from Carboniferous deposits. Disarticulated unornamented plates described below as *Platycrinites* sp. 4 have radial ratios similar to those of this specimen.

Neither the new specimen described or that of Etheridge (in Jack & Etheridge, 1892) resolves the problem of the lack of ornamentation and other external features of the plates. Also, the tegmen and arms are unknown. It could be argued that *P. nux* is based on an internal mould and the surface ornament is unknown. However, future collections in these areas should provide additional specimens to support the acceptance of *P. nux*.

**Platycrinites testudo** Campbell & Bein, 1971
(Fig. 13)

*Platycrinus* sp. Etheridge, 1892: 131, pl. 20, fig 8.
*Platycrinites testudo* Campbell & Bein, 1971: 430, pl. 51, figs 10-21.
*Platycrinites*? *crokeri* Campbell & Bein, 1971: 433, pl. 49, figs 9-15; pl. 51, figs 3-4.
*Platycrinites*? sp. 1 Campbell & Bein, 1971: 434, pl. 51, figs 1-2.

MATERIAL. MMF33433, 33437, 33438, 33441, 33445-334552, 33607; AMS F59512, 59513, 59516, 65664, 104701, 104702 from the late Tournaisian Namoi Formation, near Barraba, NSW; collected by J. Irving.

REMARKS. The nodose ornament of previously illustrated specimens indicates the variation in *P. testudo*. New specimens from the Namoi Formation support this interpretation and show additional variation in the size and alignment of the nodes and ornamentation on the radials as well as the size and arrangement of the ornamentation on the tegmen plates.

The incomplete specimen illustrated by Etheridge (1892: 20, fig. 8) was described as 4 plates of a basal circlet, but it is 2 radials with distal tegmen plate and a proximal part of the basal circlet. The radial facet is visible on the radial to the right centre and the inverted V of the nodose ornament points to the facet on the radial to the left of centre.

**Platycrinites** sp. 1
(Fig. 14F-H)

MATERIAL. MMF33440, 33442, 33443 and 33453 from the late Tournaisian Namoi Formation near Barraba, NSW.

DESCRIPTION. Cup bowl-shaped, 25mm long (crushed), 12-25.2mm wide (18.6 av.), fine granular or vermiform ornament. Basal circlet low conical, widely flaring; plates fused. Radials 5, 16.1mm long, 13.1mm wide, weakly convex longitudinally, gently convex transversely, shoulders flat to laterally sloping. Radial facet angustary, 5.4mm wide, crescent-shaped, moderately convex aborally. Primibrach axillary, concave longitudinally, moderately convex transversely. Stem facet elliptical, relatively small, 3.4 × 4.4mm. Proximal columnal with convex latus. Arms, tegmen and stem unknown.

REMARKS. *Playtcrinites* sp. 1 differs from *P. testudo* by lacking the coarse nodose ornamentation, having a more upflaring basal circlet and relatively smaller stem facet. It differs from *P.*? sp. 2 of Campbell & Bein (1971) by being more equidimensional, lacking the pustulose ornament and having shallower radial facets.

The specimens are all distorted and cracked from compaction.

**Platycrinites** sp. 2
(Fig. 14A)

MATERIAL. QMF38946 from QML508, late Tournaisian, Malchi Formation.

DESCRIPTION. Radial large, 12.8mm long, 13.6mm wide, gently convex longitudinally and transversely, thin, with fine granular ornament; radial facet angustary, projecting outward from radial surface, deep, horseshoe-shaped, strongly convex outer edge, transverse ridge wide, gently rounded, ends elevated slightly.

REMARKS. The fine granular ornament of *Platycrintes* sp. 2 readily distinguishes it from *P. testudo*. The projected horseshoe-shaped facet is much deeper and more projected than that of *P.* sp. 1. Lacking the rest of the cup and tegmen it is left in open nomenclature.

**Platycrinites** sp. 3
(Fig. 14D,E)

MATERIAL. Basal circlet and partial radials QMF38947 and partial radial plate, QMF38948, from QML508, late Tournaisian, Malchi Formation.

DESCRIPTION. Basal circlet bowl-shaped, thin, unornamented; plates fused. Radial large,

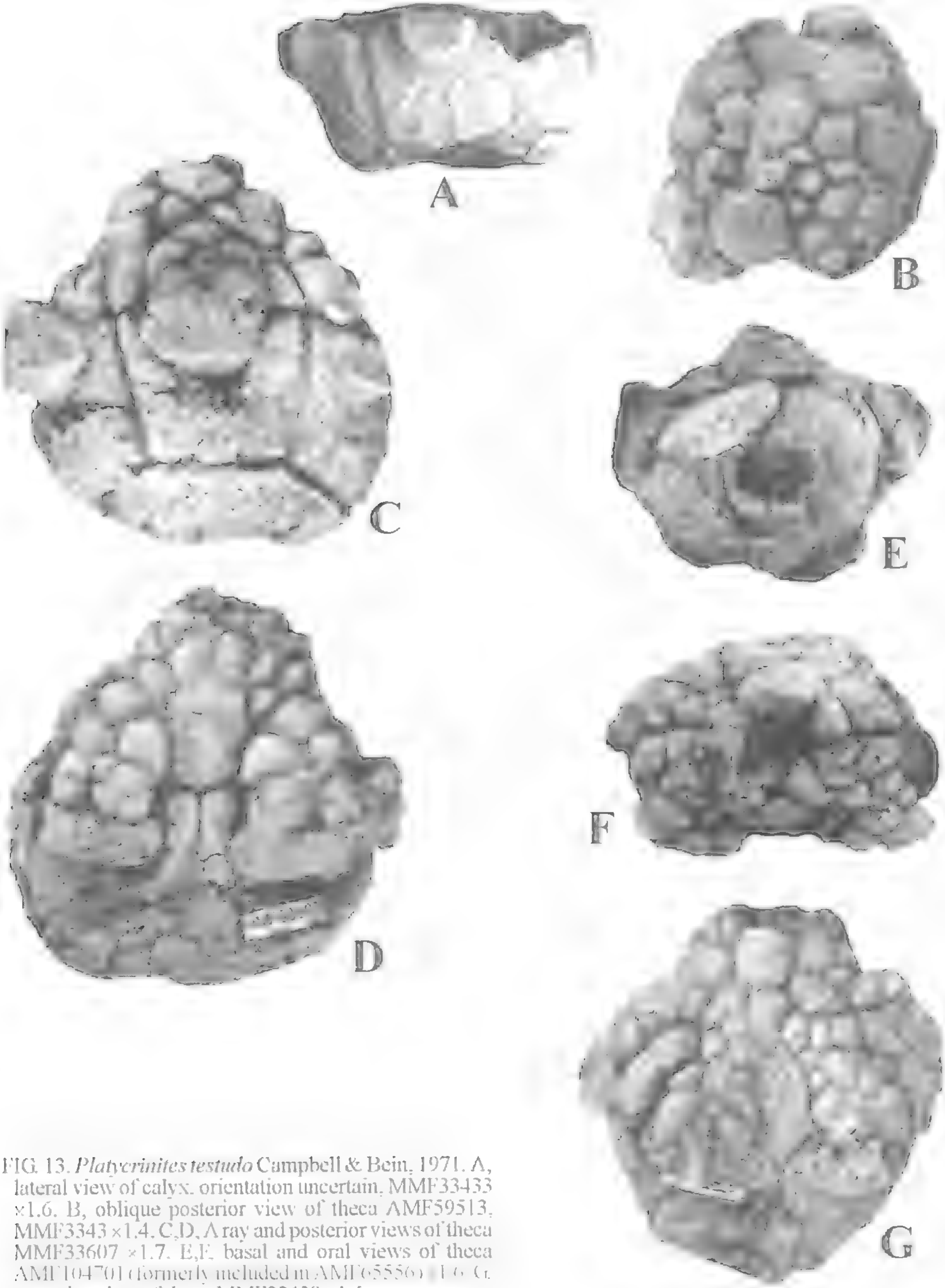



FIG. 13. *Platycrinites testudo* Campbell & Bein, 1971. A, lateral view of calyx, orientation uncertain, MMF33433 ×1.6. B, oblique posterior view of theca AMF59513, MMF3343 ×1.4. C,D, A ray and posterior views of theca MMF33607 ×1.7. E,F, basal and oral views of theca AMF104701 (formerly included in AMF65556) ×1.6. G, posterior view of theca MMF33438 ×1.6.

15.5mm long (incomplete), 15.5mm wide, thin, smooth; angustary radial facet strongly convex outwardly, slightly elevated above radial surface, small inwardly pointed V-shaped ridges at outer ends of transverse ridge. Stem facet small, 2.0 × 2.4mm, elliptical outline, with narrow crenularium.

REMARKS. *Platycrinites* sp. 3 differs from *P. testudo*, *P.* sp. 1 and *P.* sp. 2 by lacking ornament. The specimens are fractured and incomplete. They are illustrated to show the variation in the platycrinitids of eastern Australia.

**Platycrinites** sp. 4
(Fig. 14B,C)

MATERIAL. Partial basal circlet QMF38949 and partial radials QMF38950 from QML508, late Tournaisian, Malchi Fomation.

REMARKS. The basal circlet is an internal mould with the bare edges of parts of the exterior surface. It is uncrushed, high conical and thin. The thin partial radials are very elongate, unornamented and straight longitudinally. These specimens, if from one species, would have similar shape and proportions to *P. nux*, and the specimen would be tentatively referred to *P. nux* from the Caswell Creek Group.

**Camerate** indet.

*Crinoid calyx* Etheridge in Jack & Etheridge, 1892: 210, pl. 44, fig. 8.

MATERIAL. QMF1194, late Tournaisian ?Malchi Formation, Rockhampton District. Collected by C.W. De Vis.

REMARKS. The weathered internal mould of a partial calyx reported by Etheridge (in Jack & Etheridge, 1892) is an indeterminate camerate. Plate sutures are indistinguishable but the long tegmen shows parts of the ambulacral trackways of two rays. Etheridge (in Jack & Etheridge, 1892) reported the specimen from the Gympie Beds, now considered to probably be from the Malchi Formation.

Subclass DISPARIDA Moore & Laudon, 1943
Superfamily ALLAGECRINOIDEA Carpenter & Etheridge, 1881
Family ALLAGECRINIDAE
Carpenter & Etheridge, 1881

**Litocrinus** Lane & Sevastopulo, 1982

TYPE SPECIES. *Kallimorphocrinus punctatus* Lane & Sevastopulo, 1982 from the Visean New Providence Shale of Tennessee; by original designation.

**Litocrinus** sp.
(Fig. 15D-F)

MATERIAL. QMF39022, 39075 from QML878, Visean Baywulla Formation.

DESCRIPTION. Cup conical, 0.65mm long, 0.8mm wide. Basal circlet fused, 0.15mm long, 0.5mm wide. Radials straight longitudinally, moderately convex transversely, moderately flaring; radial facets convex outward, subhorizontal. Small anal notch. Oral circlet moderately arched. Orals 5, concave; posterior oral larger, separating BC and DE orals.

REMARKS. The cup of QMF39022 is coated with small secondary crystals masking plate sutures and giving the specimen a false ornament. The specimen has a higher basal circlet than *L. scoticus* and is not as elongate as *L. extensus*, both described from the Visean of Scotland (Wright, 1932, 1952). It is not as elongate as *L. angulatus* and *L. tintinabulum*, both from the Visean Nunn Shale of New Mexico (Strimple & Koenig, 1956). It also lacks the concave cup walls of *L. protuberans* and *L. pansus*, both reported from the Permian of Western Australia (Webster & Jell, 1992). It may represent a new species, but is an inappropriate specimen to serve as a type. The smaller immature specimen QMF39075, is 0.55mm long and 0.45mm wide, weathered and shows poor plate margins. This is the first report of *Litocrinus* from the Carboniferous of Australia.

Superfamily BELEMNOCRINOIDEA
S.A. Miller, 1883
Family SYNBATHOCRINIDAE
S.A. Miller, 1889

**Synbathocrinus** Phillips, 1836

TYPE SPECIES. *Synbathocrinus conicus* Phllips, 1836 from the Tournaisian of England; by monotypy.

**Synbathocrinus ogivalis** de Koninck, 1878
(Fig. 15A-C)

*Synbathocrinus ogivalis* de Koninck, 1878: 158, pl. 6, figs 1-1b; 1898: 121, pl. 6, figs 1-1b. Bassler & Moodey, 1943: 696.
*Synbathocrinus* sp. Campbell & Bein, 1971: 424, pl. 49, figs 16-21, text-fig. 5. Webster, 1977 164.

MATERIAL. MMF33432 from the late Tournaisian Namoi Formation near Barraba, NSW.

DESCRIPTION. See de Koninck (1878, 1898) and Campbell & Bein (1971).

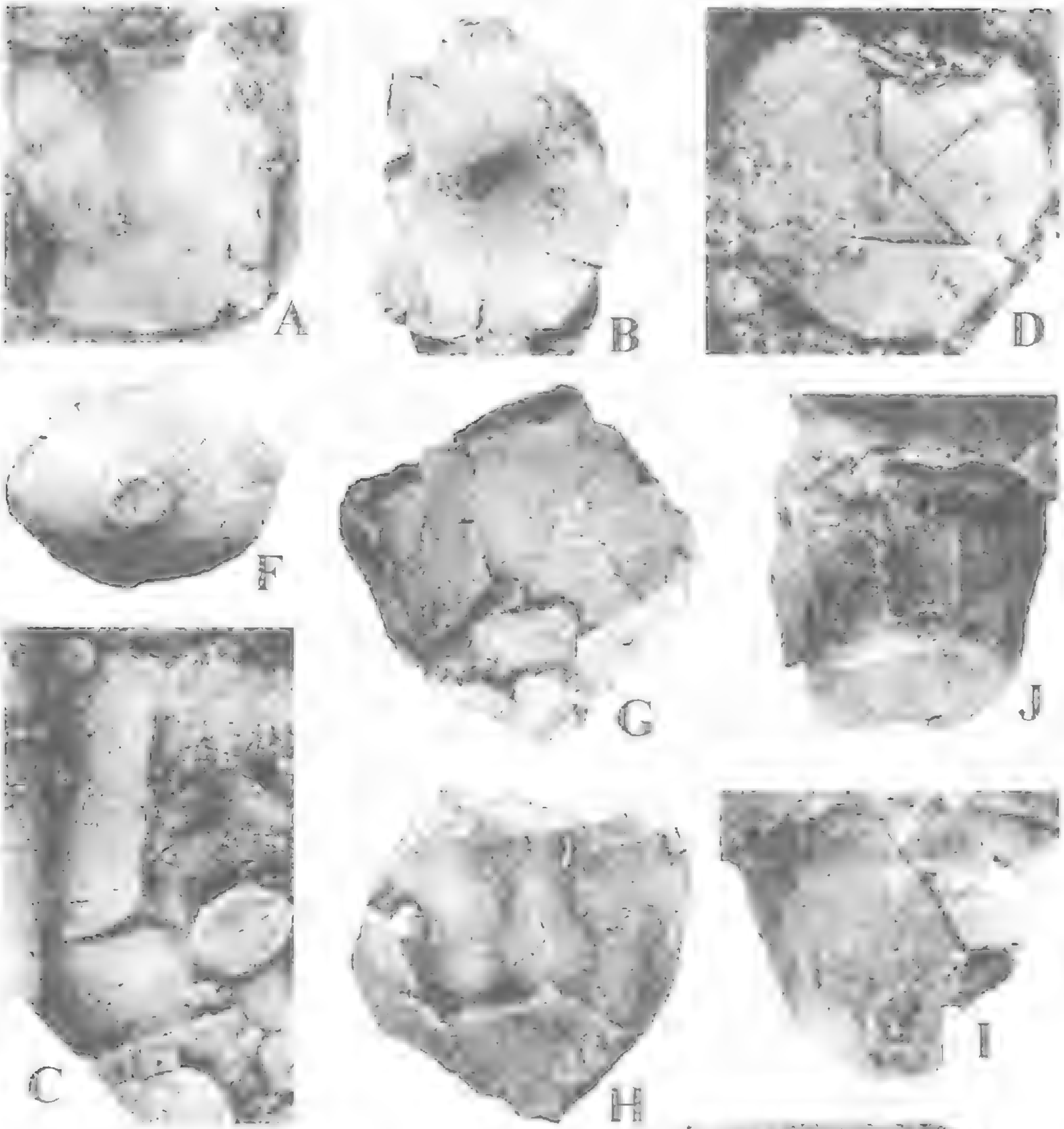
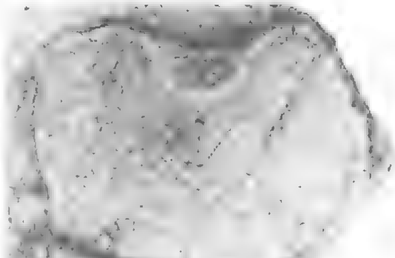



FIG. 14. A, *Platycrinites* sp. 2, lateral view of radial QMF38946 ×3.2. B,C, *Platycrinites* sp. 4. B, interior view of partial basal circlet QMF38949 ×2.5. C, lateral view of partial radial and associated columnal QMF38950 ×2.5. D,E, *Platycrinites* sp. 3. D, view of disarticulated basal circlet and radials QMF38947 ×2.9. E, lateral view of partial radial QMF38948 ×2.7. F-H, *Platycrinites* sp. 1. F, basal view of slightly distorted basal circlet MMF33443 ×1.7. G,H, lateral views of weathered partial interior and exterior of opposite side of crushed calyx MMF33440, X1.7. I,J, *Platycrinites nux*? (Etheridge, 1892), lateral views of calyx interior, orientation uncertain. GSQF10870 ×1.5



REMARKS. *Synbathocrinus ogivalis* was reported by de Koninck (1878) from an unknown horizon at Burragood, Paterson River, NSW. As noted by Campbell & Bein (1971), it probably came from the Lower Carboniferous. De Koninck's original description is minimal and his illustrations are stylised. However, they are sufficient to define and recognise the species. De Koninck (1878) mistakenly reported the basal circlet to be a single plate for all species of *Synbathocrinus* including *S. ogivalis*, whereas Campbell & Bein (1971) showed 3 plates in their *S.* sp. Both de Koninck's (1878) and Campbell and Bein's (1971) descriptions are considered correct for the specimens investigated and show the variation in *S. ogivalis*. The basal circlet of *Synbathocrinus* is highly variable within most species known from multiple specimens. Webster & Lane (1987) reported the basal circlet of 2 undesignated species in the late Tournaisian Anchor Limestone of southern Nevada to vary from 1-4 plates. Two Artinskian species from Western Australia (Webster, 1987) varied from 1-4 plates in *S. campanulatus* and from 1-3 in *S. constrictus*. The specimen illustrated herein has 3 plates in the basal circlet, with the EA basal azygous, but the sutures are difficult to define, because of partial fusing and recrystallisation.

The type specimen of *S. ogivalis* is presumed lost in the Garden Palace fire of 1886. Therefore, ANU18893, (Campbell & Bein, 1971, pl. 49, figs 16-18) is designated the neotype.

Subclass CLADIDA Moore & Laudon, 1943
Order CYATHOCRINIDA Bather, 1899
Superfamily CYATHOCRINITOIDEA Bassler, 1938
Family EUSPIROCRINIDAE Bather, 1890

## **Neerkolocrinus** gen. nov.

TYPE SPECIES. *Neerkolocrinus typus* from the Westphalian Neerkol Formation, Rockhampton.

ETYMOLOGY. For the Neerkol Formation.

DIAGNOSIS. Crown robust, expanding gently distally; cup medium to high bowl-shaped, with upflared basals; plate inflated, with stellate ridge ornament on basals and radials and fine node ornament on cup plates continuing on brachials; 5 anals in cup; prominent anal tube tapering distally above posterior interray; at least 10 arms, branching isotomously on 6th primibrach; at least one ramule on 3rd secundibrach in some rays; brachials rectilinear, strongly rounded transversely, lacking pinnules.

REMARKS. *Neerkolocrinus* shows some relationship to both euspirocrinids and botryocrinids. Genera assigned to both the euspirocrinids and botryocrinids have a conical or bowl-shaped cup, lacking stellate ornamentation and 1-4 anals. The presence of the proximal 1/2 of the first 2 tube plates below the radial summit does not alter the number of anals in the cup significantly, but is considered a primitive condition. First branching of the arms on the 6th primibrach is also considered a primitive condition for such a young form of euspirocrinid or botryocrinid. The tapered anal tube above the posterior interray is present in some euspirocrinids (*Euspirocrinus* and *Parisocrinus*), whereas most botryocrinids have longer or recurved anal tubes. The radianal is beneath or below to the left of the C radial in most euspirocrinids and botryocrinids. Botryocrinids typically have ramules and the brachials lack cover plates, which euspirocrinids and *Neerkolocrinus* have. Muscular articulation and an internal axial canal in the brachials of *Neerkolocrinus* also show relationships to the euspirocrinids rather than the botryocrinids.

Euspirocrinids may be divided into 3 groups based on cup shape. *Ampheristocrinus*, *Closterocrinus*, *Parisocrinus* and *Zygotocrinus* have narrow, long cone-shaped cups. *Caelocrinus* and *Vasocrinus* have short conical to bowl-shaped cups and *Euspirocrinus* and *Neerkolocrinus* have long wide bowl-shaped cups. *Neerkolocrinus* is distinguished from *Euspirocrinus* by the more bowl-shaped cup, more distal 1st branching of the arms, stellate ridge ornament and continuation of fine node ornament onto the brachials.

### **Neerkolocrinus typus** sp. nov.
(Figs 16,17A,B)

ETYMOLOGY. Latin *typus*, model or example; the type species.

MATERIAL. HOLOTYPE: GSQF10872 from GSQLK106, late Namurian or early Westphalian Neerkol Formation.

DIAGNOSIS. As for genus.

DESCRIPTION. Crown robust, elongate, flaring upward gently, 43.9mm long (incomplete), 19.4-23mm wide (21.2mm av.). Cup medium high bowl-shaped, plates inflated, 17.6mm long, 13.6-23mm wide (18.3mm av.); ornament of stellate ridges to adjoining plates on basals and radials, ray ridges more strongly developed than non-ray ridges; fine granular nodes with some alignment parallel to plate margins, nodes continuing on all brachials. Infrabasal circlet diameter 11.8mm

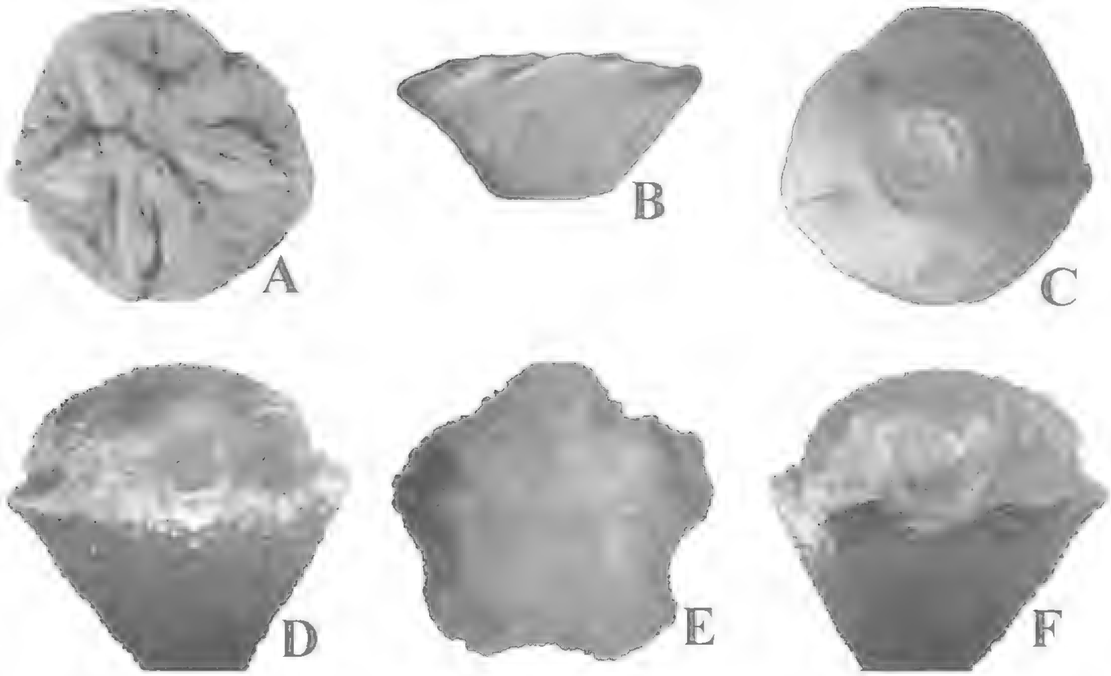


FIG. 15. A-C, *Synbathocrinus ogivalis* de Koninck, 1878, oral, posterior and basal views of cup MMF33432 ×4.2. D-F, *Litocrinus* sp., A ray, oral and posterior views of cup QMF39022 ×50.

internally. Infrabasals 5, slightly inflated, forming base of cup, upflared, visible in lateral view, distal tips forming base of cup walls. Basals 5, equidimensional, 9.5mm long and wide, moderately convex longitudinally and transversely, hexagonal; BC basal heptagonal supporting primanal on left shoulder; CD basal octagonal supporting first and second anals on right side and shoulder. Radials 5, slightly wider (10.2mm) than long (9.1mm), moderately convex longitudinally and transversely, subvertical to slightly incurved. Radial facet angustary, horseshoe-shaped, strongly declivate. Anals 5 in cup. Primanal pentagonal, below and left of C radial, also adjoining BC and CD basals, 2nd and 3rd anals. Second anal largest, hexagonal, adjoining primanal, CD basal, D radial, 2 anal tube plates and 3rd anal. Basal 1/2 of 4th and 5th anals below summit of radial facets. Anal tube extending well above radial summit over posterior interray, tapering distally. Arms at least 10, if isotomous branching in all rays on 6th primibrachs as in D and E rays. Brachials uniserial, rectilinear, strongly convex transversely, wider than long proximally, distally subcircular transversely, nonpinnular; primibrachs 3.2mm long, 5.5mm wide. Third secundibrach giving off ramule in D ray. All brachial facets with transverse ridge across approximate middle of facet, deep transversely elongate ligament pit on outer margin, very small internal axial canal in middle of transverse ridge, elevated adoral area between transverse ridge and ambulacral groove, large muscle areas on inner margins, triarthrial articulation. Ambulacral groove deep V-shaped, notched on both sides; small cover plates not preserved.

REMARKS. The type is preserved as external and internal moulds of a partial crown compressed along the A-CD plane of symmetry.

## **Kopriacrinus** gen. nov.

TYPE SPECIES. *Kopriacrinus mckellari* gen. et sp. nov. from the Westphalian Neerkol Formation, W of Rockhampton.

ETYMOLOGY. Greek *Kopria*, dunghill; refers to the appearance of the cup as a cluster of pellets or a composite fecal pellet.

DIAGNOSIS. Crown small; cup high cone-shaped; plates inflated; sutures impressed, apical pits; radial facet angustary, declivate; 3 anals; tegmen plates large, minimum 10; quadrate orals separated by large ambulacrals; tegmen sub-horizontal or projecting slightly above radial

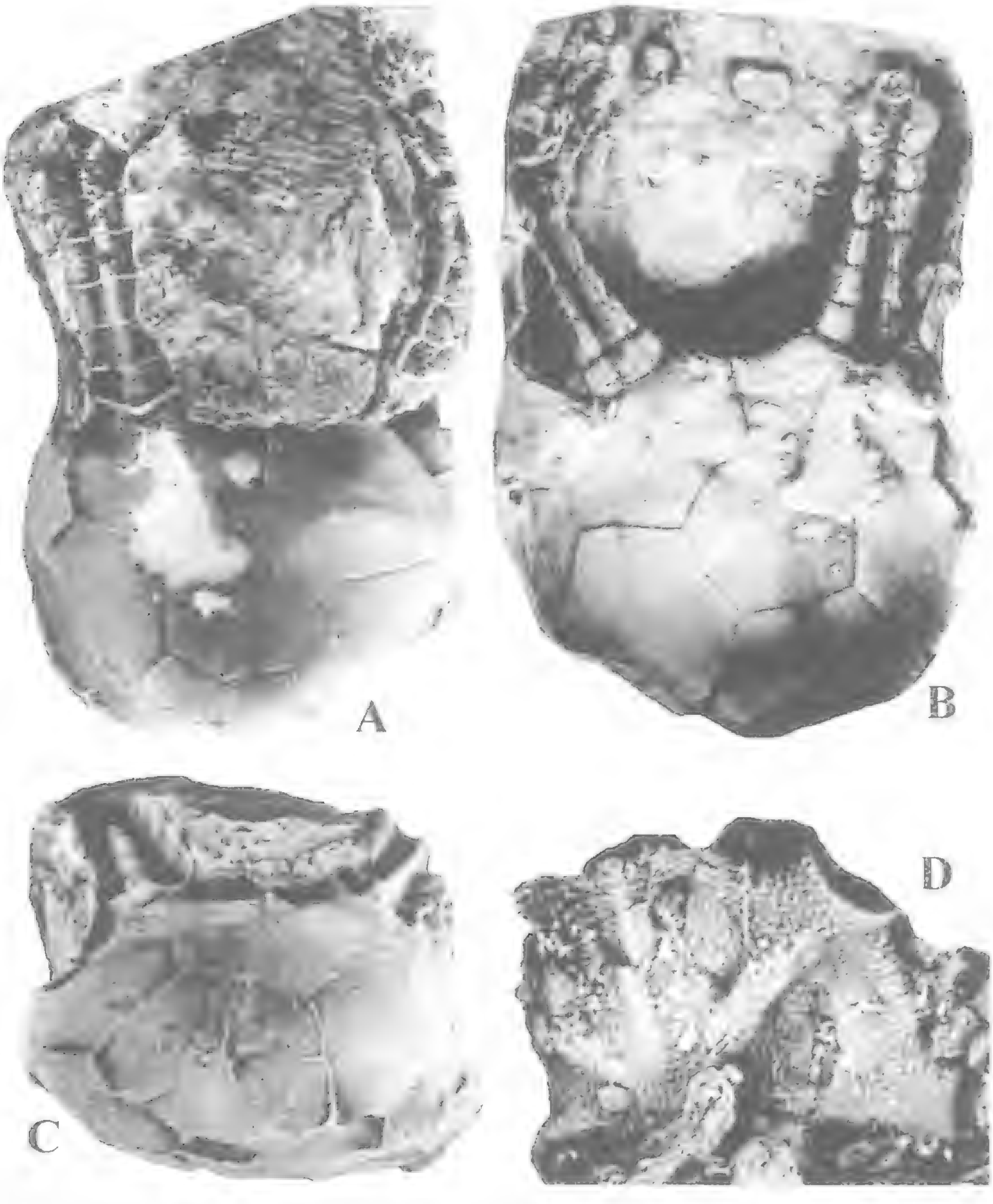
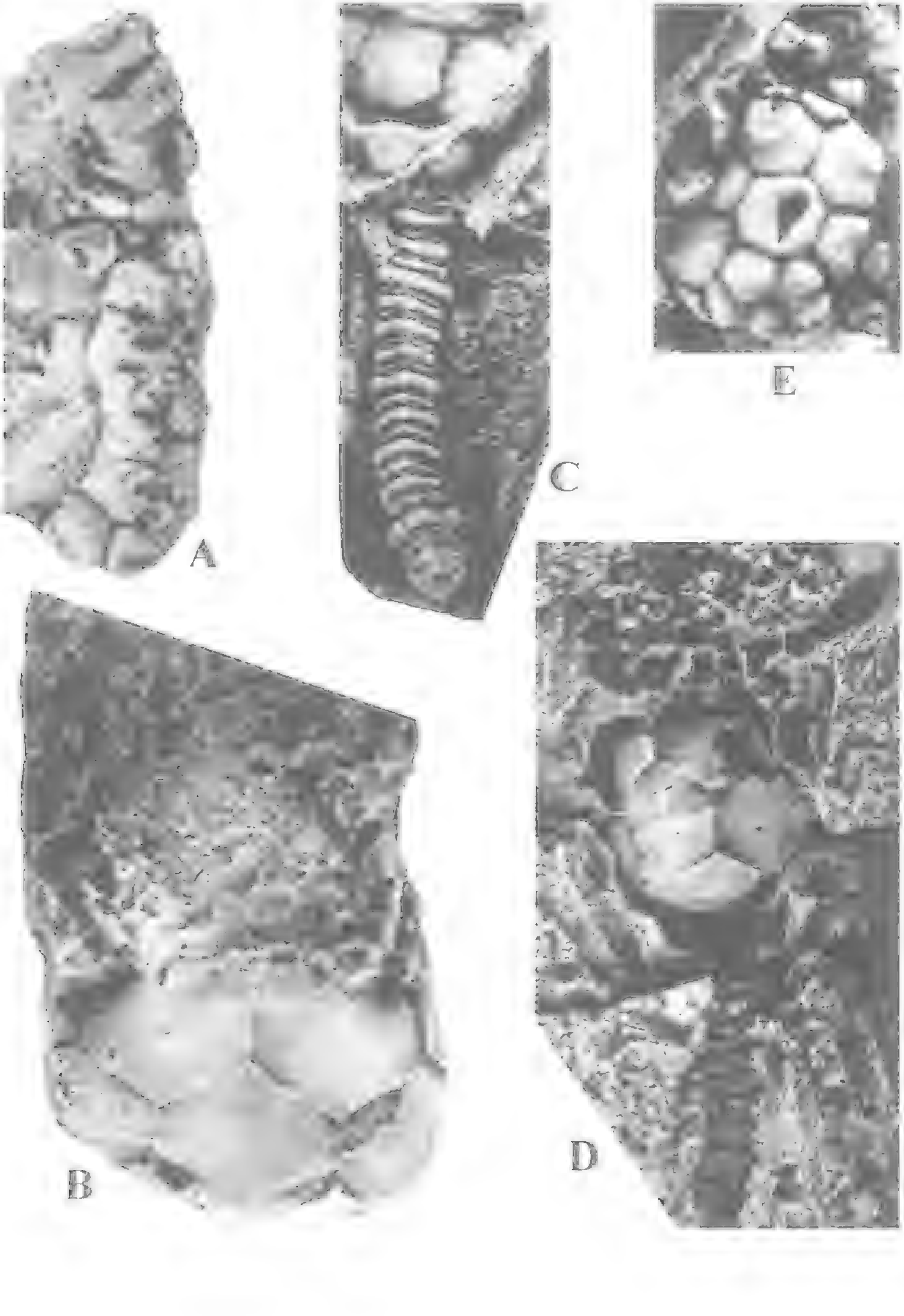



FIG. 16. *Neerkolocrinus typus* gen. et sp. nov., holotype, GSQF10872. A, B-C interray view of internal mould ×2.8. B, D-E interray view of external moul ×2.8. C, basal view of internal mould ×2.9. D, C ray view of external surface of cup ×3.9.

FIG. 17. (Opposite) A,B, *Neerkolocrinus typus* gen. et sp. nov., holotype, GSQF10872. A, lateral view of external surface of partial arm ×3.7. B, D-E interay view of internal mould ×2.8. C-E, *Kopriacrinus mckellari* sp. nov C,D, internal ×3.5) and external ×4.7) views of paratype GSQF10874. E, C ray view of cup with associated brachial fragments, holotype GSQF10873 ×3.7


A
B
C
D
E

summit; at least 10 arms; rectilinear brachials strongly rounded transversely; stem transversely pentagonal, heteromorphic.

REMARKS. Except for the pentagonal stem *Kopriacrinus* fits the Euspirocrinidae, which were defined by Lane & Moore (in Moore & Teichert, 1978) as having a round stem. Phylogenetic significance of this feature is uncertain, but may imply a polyphyletic origin of the family. *Kopriacrinus* differs from all genera in the family by one or more other morphologic features. It is most similar to *Vasocrinus*, which differs by having a low conical cup with large axial canals in the brachials and radials.

**Kopriacrinus mckellari** sp. nov.
(Fig. 17C-E; Table 3)

ETYMOLOGY. For R.G. McKellar in recognition of his contributions to the geology of Queensland.

MATERIAL. HOLOTYPE: GSQF10873. PARATYPE: GSQF10874 from GSQL K106, late Namurian or early Westphalian Neerkol Formation.

DESCRIPTION. Crown small, cylindrical to slightly expanding distally. Cup high cone shaped, with inflated plates, sutures impressed, apical pits. Infrabasal circlet with shallow invagination for pentagonal stem facet. Infrabasals 5, proximally horizontal, distally upflared forming base of cup wall, visible in lateral view, bulbus, strongly convex longitudinally and transversely. Basals 5, hexagonal, wider than long, straight longitudinally, moderately convex transversely, inflated, surface irregular; BD and CD basals heptagonal, with extra side adjoining anal plates. Radials 5, pentagonal, wider than long, strongly convex longitudinally and transversely, inflated, surface irregular. Radial facet angustary, declivate, projecting out from radial, horseshoe-shaped, with faint transverse ridge. Anals 3; radianal large, adjoining BC and CD basals, inflated. Anal X and right tube plate probably projecting above radial summit. Tegmen plates large, at least 10. Orals quadrate, filling radial notches, abutting large ambulacrals adorally. Ambulacrals large, expanding adorally, with longitudinal ridge. Tegmen subhorizontal or projecting slightly above radial summit. Anal tube unknown. Rectilinear brachials horseshoe- shaped transversely, straight to slightly concave longitudinally, with deep V-shaped ambulacral groove, with facets for cover plates. At least one isotomous branching of arms; probably 10 arms. Stem transversely pentagonal, heteromorphic. Noditaxis pattern N1. Columnals with large lumen, strongly convex latus.

REMARKS. The smaller holotype is an external mould of a slightly crushed cup with some associated brachials, whereas the larger paratype is an external and internal mould of a crown with disarticulated arm plates adjacent to the cup and 28.0mm of stem. The well-developed bulbous infrabasals are nearly equidimensional on the holotype, but longer than wide on the paratype.

The holotype is compressed along the AB-posterior interray/D plane. The paratype is compressed along the A-CD plane of symmetry.

Order POTERIOCRINIDA Jaekel, 1918
Superfamily POTERIOCRINITOIDEA
Austin & Austin, 1842
Family POTERIOCRINITIDAE
Austin & Austin, 1842

**'Poteriocrinites'? smithii** (Etheridge, 1892)
(Fig. 18)

*Poteriocrinus*? *smithii* Etheridge in Jack & Etheridge, 1892: 209, pl. 8, fig. 1.
*Poteriocrinites smithi* Etheridge; Bassler & Moodey, 1943: 645. Branson, 1948: 209.

MATERIAL. Plasticine cast BME15661 and plaster cast GSQF1590 stratigraphic unit uncertain, possibly from the Rockhampton Group, near Stanwell, Queensland.

DESCRIPTION. Crown elongate, 33.0mm long, 21.2mm wide (arms flaring distally). Cup bowl-shaped, with stellate ridge ornament on basals and radials. Infrabasal circlet large, proximally horizontal, bearing stem facet, distally upflared, probably formed of 5 plates. Basals large, strongly convex longitudinally and transversely, forming base of cup walls; BC basal 3.9mm long, 2.9mm wide (estimated). Radials large, 2.1mm long, 4.0mm wide (estimated), moderately convex longitudinally and transversely, subvertical, with wide laterally sloping shoulders distally. Radial facet angustary, 1.7mm wide, with strongly convex outer rim, declivate, with radiating crenulae and culmina on outer margin. Radial notches wide. Anals 3, convex longitudinally and

TABLE 3. *Kopriacrinus mckellari* measurements (mm).

| | Holotype F10873 | Paratype F10874 |
|---|---|---|
| Cup length | 8.4 | 9.4 |
| Cup width (maximum) | 7.0 | 10.4 |
| Infrabasal circlet diameter | 5.0 | 5.2 |
| Basal length | 3.1 | 5.8 |
| Basal width | 3.1 | 5.0 |
| Radial length | 3.8 | 4.4 |
| Radial width | 3.7 | 6.7 |
| Stem diameter | | 3.3 |

transversely. Radianal below C radial, pentagonal, 2.8mm long, 1.7mm wide, adjoins C radial, BC basal, infrabasal circlet, CD basal and anal X. Anal X hexagonal, large, length 2.5mm, width 2.0mm, adjoins C radial, radianal, infrabasal circlet, CD basal, D radial, right tube plate. Right tube plate rectangular, in radial circlet above anal X. Stellate ridges sharply elevated; 4 ridges radiating from the B radial downward, 2 onto each subjacent basal; 3 ridges radiating from the C radial downward, 1 each onto BC basal, radianal, anal X. One subhorizontal ridge extending laterally from anal X onto radial to right and CD basal to left.

Brachials slightly cuneate, narrow, straight longitudinally, strongly convex transversely, horseshoe-shaped transversely, with 1 very slender pinnule on long side, with medium nodes on exterior. First branching isotomous on 2nd primibrach and exotomous on 2nd secundibrach in 2 rays visible. Arms 3 per ray, 15 if all rays branch in same manner. Stem circular transversely, heteromorphic, 1.5mm diameter, 37.0mm long, incomplete. Noditaxis N3231323 proximally, $N_7$ distally; nodals cirrate, multiple cirri per nodal. Columnals wide, with well rounded latus. Cirri small, homeomorphic, transversely round.

REMARKS. The description differs considerably from that of Etheridge (in Jack & Etheridge, 1892) in recognition of the infrabasal circlet and anals. Plate sutures are difficult to determine on the casts, but are visible with magnification as the stellate ridges are slightly offset. The original interpretation is that the visible part of the cup consists of 2 partial radials, 1 on either side of a centrally complete radial; the underlying very wide basals are fractured and only the distal tips of 2 of the infrabasals are visible at the top of the stem. If this interpretation is correct, then the stellate ridge ornament varies considerably on the different radials and basals. The consistency in the stellate ridge ornament is accounted for in the new interpretation.

The specimen is not a *Poteriocrinites*. It probably represents a new genus of the Poteriocrinitidae, based on the arm branching pattern and cup ornament, both of which differ significantly from all other genera assigned to the family. In hopes the original will be found or other specimens discovered we do not alter the original citation.

Etheridge (in Jack & Etheridge, 1892) reported the specimen to be an impression in a hard sandstone. Attempts to locate the original specimen failed but resulted in location of the materials listed above. The original specimen is apparently lost. A note with the plaster cast, GSQF1590, reported the original specimen was loaned to F.A. Bather and returned to the Geological Survey of Queensland in 1915 with three plaster casts, only one of which remains. Etheridge's figure was drawn from an earlier cast, perhaps one of the two plasticine casts in the British Museum (E15661).

FIG. 18. '*Poteriocrinites*'? *smithii* (Etheridge, 1892), C ray view of plasticine cast of holotype, BME15661 ×1.7.

The stratigraphic position of '*P.*'? *smithii* is uncertain. Etheridge (in Jack & Etheridge, 1892) reported the specimen from the Gympie Beds in the vicinity of Stanwell. As mapped by Dunstan

(1898) the Gympie Formation was the wide-spread basal unit of the Carboniferous in the Stanwell area. Currently, the Gympie Group is restricted to the Middle Permian of the Gympie Block (Day et al., 1982) and not recognised in the Stanwell area. There are several fossiliferous horizons in the Carboniferous and Permian in the vicinity of Stanwell. Without the original specimen the lithology cannot be matched and age of the specimen is in question.

Superfamily SCYTALOCRINOIDEA
Moore & Laudon, 1943
Family SCYTALOCRINIDAE
Moore & Laudon, 1943

**Prininocrinus** Goldring, 1938

TYPE SPECIES. *Prininocrinus robustus* Goldring, 1938 from the Late Devonian of Canada; by original designation.

REMARKS. The A ray of the holotype of *Prininocrinus robustus* lacks the arm above the 1st primibrach and Goldring (1938) noted that 3 other rays branch on the 2nd primibrach. Furthermore, she described one of the paratypes as having 3 primibrachs in one ray, which could be the A ray. Orientation of the specimen did not allow unquestioned identification of the ray. Thus, it is unknown if *Prininocrinus* has an atomous A ray or branched at some level above the 3rd primibrach. An atomous A ray is a primitive character of some Scytalocrinidae (*Histocrinus*, *Hypselocrinus*) among other primitive inadunates. However, it is not an invariable character, as the A ray branches (often on primibrach 6 or higher) on some species assigned to these genera. Although listed under the Scytalocrinidae *Prininocrinus* was incorrectly placed in synonomy with *Scytalocrinus* (Moore & Strimple, in Moore & Teichert, 1978:640), as the arms of *Scytalocrinus* branch on the single primibrach in all rays. *Prininocrinus* is here accepted and considered to have an atomous or branched A ray.

**Prininocrinus namoiensis** sp. nov.

*Histocrinus* sp. Campbell & Bein, 1971: 423, pl. 50, figs 8-9, text-fig. 4.

ETYMOLOGY. From the Namoi Formation.

MATERIAL. HOLOTYPE: ANU21344 from the late Tournaisian Namoi Formation, Crinoid Creek, near Barraba, NSW.

DIAGNOSIS. Crown slender, elongate; cup low bowl-shaped, distal tips of basals visible in lateral view; 3 anals in cup; radial facets plenary; brachials strongly convex transversely, rectilinear, isotomous branching on 2nd primibrach in all rays except atomous A ray; pinnules very slender, elongate.

DESCRIPTION. See Campbell & Bein (1971: 423)

REMARKS. The partial crown assigned to *Histocrinus* by Campbell & Bein (1971) is reassigned to *Prininocrinus* because the brachials are rectilinear not cuneate as in *Histocrinus* (Kammer & Ausich, 1992). *Prininocrinus namoiensis* has a low bowl-shaped cup with the distal tips of the infrabasals visible in lateral view, 3 anals in the cup and rectilinear strongly rounded brachials. *P. namoiensis* differs from *P. robustus* by having a slightly shorter cup, less robust arms and more slender pinnules. The infrabasals, essentially confined to the basal plane of the cup (except for the distal upflared tips), and the intermediate position of the 3 anals (primanal moved wholely or partly into the CD interray position) are slightly advanced conditions in *P. robustus* and *P. namoiensis*.

**Scytalocrinid**? indet.
(Fig. 11)

MATERIAL. QMF38958, locality and horizon unknown in NSW, probably late Tournaisian Namoi Formation. Collected by G.M. Philip

DESCRIPTION. Cup small, truncated cone-shaped, no ornament. Infrabasal circlet forming truncated base proximally, weakly flared distally forming lower 1/4 of cup wall. Basals subequal length and width, straight longitudinally, gently convex transversely, gently flaring distally; CD basal truncated distally for reception of anal X. Radials gently flaring longitudinally, moderately convex transversely. Radial facet plenary, projecting slightly. Primibrach widest at base, blade-shaped proximally, constricted medially, strongly convex transversely shortly distal to base, concave longitudinally; distal end unknown. Proximal stem heteromorphic, with noditaxis N1, becoming homeomorphic distally. Columnals circular transversely; latus strongly convex.

REMARKS. This small partial crown is crushed and the cup plates are partly disarticulated with the proximal end of the radial covered by subjacent basals. The truncated end of the CD basal is narrow, suggesting there was a radianal to the lower right of anal X and 3 anals in the cup. Cup and primibrach shapes, in conjunction with the

plenary radial facet, suggest affinity with Scytalocrinidae such as *Hydriocrinus* and *Hypselocrinus* but without the arms and anal series no generic assignment can be made. The specimen is associated with an unnamed new genus of rhodocrinitid and *Dichocrinus* cf. *D. laudoni* on a small slab.

Superfamily ERISOCRINOIDEA Wachsmuth & Springer, 1886
Family GRAPHIOCRINIDAE Wachsmuth & Springer, 1886

**Holcocrinus** Kirk, 1945

TYPE SPECIES. *Graphiocrinus longicirrifer* Wachsmuth & Springer, 1890 from the Tournaisian Hampton Formation, Iowa; by original designation.

**Holcocrinus barrabaensis** sp. nov.
(Fig. 19)

ETYMOLOGY. From Barraba, NSW

MATERIAL. HOLOTYPE: MMF33608 (AMSF59510 and 59511 are casts of the type) from the late Tournaisian Namoi Formation, Crinoid Creek, near Barraba, NSW; found by J. Irving.

DIAGNOSIS. Crown elongate; cup truncated medium cone, primibrachs axillary, intermediate length; brachials intermediate length, moderately cuneate; unornamented.

DESCRIPTION. Crown elongate, 54.9mm long (incomplete), 21.5mm wide. Cup truncated medium cone, 7.0mm long, 7.5-11.5mm wide (9.5mm av.), lacking ornamentation. Infrabasals 5, horizontal proximally, upflared distally, visible in lateral view. Basals 5, 3.6mm long, 3.8mm wide, hexagonal, except CD basal heptagonal, gently convex transversely and longitudinally. Radials 5, 5.8mm long, 4.1mm wide, moderately convex transversely, gently convex longitudinally. Radial facet plenary. Single anal, widest distally, 4.2mm long, 3.8mm wide, slightly convex transversely and longitudinally, projecting slightly above radial summit. Axillary single primibrachs equidimensional, 5.8mm, strongly convex transversely, concave longitudinally, hourglass-shaped. Secundibrachs cuneate, short, moderately convex transversely, concave longitudinally, faintly staggered, probably with pinnule on shoulder of longer side. Arms 10, 2 per ray, branching isotomous. Stem homeomorphic, 58.0mm preserved, proximally transversely pentagonal for 14.5mm (5.0mm diameter), round distally (3.7mm diameter). Tegmen unknown.


FIG.19. *Holcocrinus barrabaensis* sp. nov., A,B, posterior (AMSF59511) and anterior (AMSF59510) views, ×1.

REMARKS. The holotype was embedded in mudstone. A cast (AMF59510) shows 58.0mm of stem. Part of the stem is now missing on the original.

Webster (1997) noted that *Holcocrinus* has cuneate brachials and suggested that it belongs to a clade of conservative inadunates retaining a conical cup. The infrabasals forming the truncated base of the cup with only the distal tips visible in lateral view and a single anal are more advanced features within this conservative clade. The crown of *H. barrabaensis* is crushed normal to the BC-DE plane.

*Holcocrinus barrabaensis* is distinguished within the genus by having a truncated medium conical

cup, brachials of intermediate length and lacking ornamentation. The cup of *H. wachsmuthi* (Meek & Worthen, 1861) is a much higher truncated cone. *H. spinobrachiatus* (Hall, 1861) has a broader medium bowl shape and all other species have low bowl-shaped cups. Brachials of *H. longicirrifer* (Wachsmuth & Springer in Miller, 1889) are very short and strongly cuneate, whereas those of *H. wachsmuthi* are longer, triangular and nearly biserial. Brachials of *H. nodobrachiatus* (Hall, 1861) and *H. spinobrachiatus* have short nodes or spines on the distal ends of the moderately cuneate brachials. Brachials of *H. barrabaensis* lack the spines, are longer than those of *H. longicirrifer* and shorter than those of *H. spinobrachiatus*. The axillary primibrachs of *H. smythi* are much longer than those of *H. barrabaensis* which are longer than those of *H. longicirrifer*.

**Poteriocrininid** cup indet.

Crinoid allied to *Stemmatocrinus* Etheridge in Jack & Etheridge, 1892: 206, pl. 44, fig 7.

MATERIAL. QMF1196 probably from the late Tournaisian Malchi Formation, Rockhampton District. Collected by C.W. De Vis.

REMARKS. An indeterminate poteriocrininid cup 10.6mm wide is a slightly distorted internal mould and parts of 3 weathered radial facets. The basal circlet is subhorizontal and formed of 5 plates. Basals were horizontal proximally, upturned on the distal tips. One basal is wider than the other 4 and presumably had 1 or 2 anals above it. Cup walls were largely formed by the subvertical radials. Etheridge (in Jack & Etheridge, 1892) apparently thought the specimen lacked an anal plate when he considered it allied to *Stemmatocrinus* (=*Erisocrinus*). The cup could belong to any number of the poteriocrininids, depending on the number of anals and is considered indeterminate. Etheridge (in Jack & Etheridge, 1892) reported the specimen from the Gympie Beds, now considered to probably be from the Malchi Formation.

**Poteriocrininid** arms indet. #1
(Fig. 20A)

Arms of crinoid Etheridge in Jack & Etheridge, 1892: 210, pl. 7, fig. 8. Parfrey, 1996: 242.

MATERIAL. GSQF1588, external mould of a partial set of arms from the Tournaisian Rockhampton Group, Stony Creek, Stanwell. Collected by J. Smith.

DESCRIPTION. Partial set of 10 arms of at least 3 rays, 27.0mm long, 22.0mm wide, flaring distally. Brachials smooth, no ornament, weakly cuneate, straight longitudinally, strongly convex

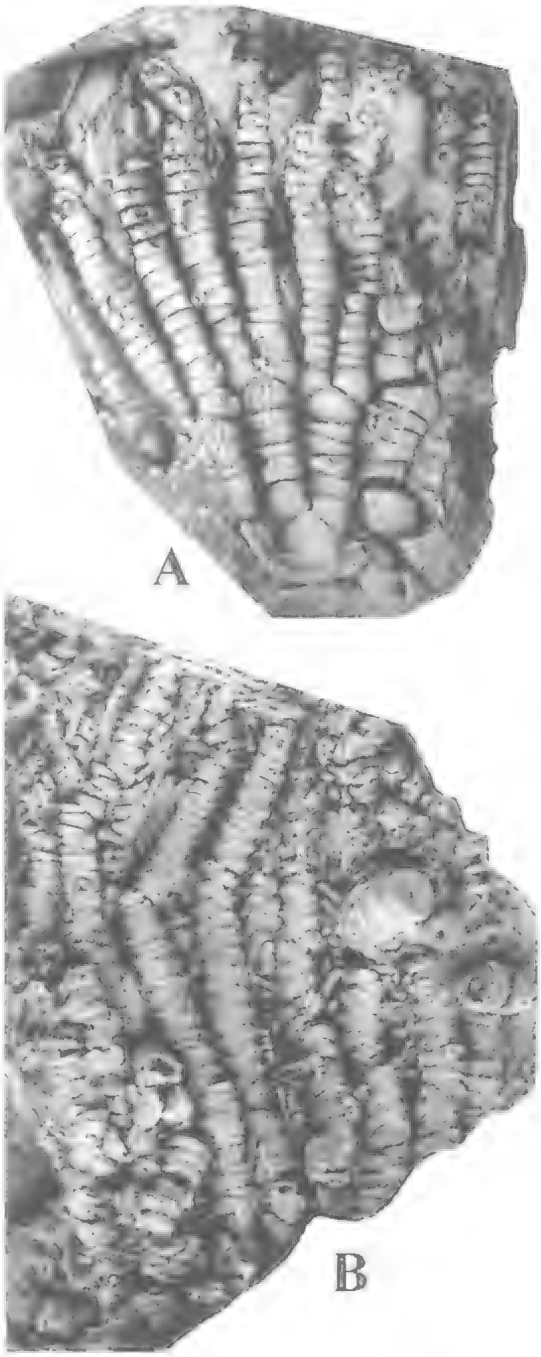



FIG. 20. A, Poteriocrininid indet. arms #1, lateral view of arms GSQF1588, ×2.5. B, Poteriocrininid indet. arms #2, lateral view of arms GSQF1587, ×2.

transversely, deep, U-shaped in transverse section, with slender pinnule on longer side. Ambulacral groove small, V-shaped. First secundibrach much longer than following secundibrachs, formed by fusing of 2 brachials. Isotomous branching on only primibrach preserved and axillary secundibrach 6.

REMARKS. The brachial shape, branching pattern and longer 1st secundibrach are common to aphelecrinids to which this specimen may be related. The aphelecrinids are most common in Tournaisian and early Visean, strata of the United States and Scotland (Bassler & Moodey, 1943; Webster, 1973, 1977, 1986, 1988, 1993).

The specimen is re-illustrated because the original does not show the distal part of the arms and is, in part, a reconstruction of part of the arms that are masked by matrix. No part of the cup is recognisable in the few fragmentary plates at the base of the arms.

**Poteriocrininid** arms indet. #2
(Fig. 20B)

Arms of crinoid Etheridge in Jack & Etheridge, 1892: 210, pl. 7, fig. 7. Parfrey, 1996: 242.

MATERIAL. GSQF1587, external mould of partial set of arms, from the Rockhampton Group, Rhynchonella Gully, Stanwell. Collected by J. Smith.

DESCRIPTION. Partial set of 8 arms, 34.6mm long, 30.8mm wide. Brachials weakly cuneate, straight longitudinally, strongly convex transversely, nearly circular in transverse section, bear transverse row of 3-5 coarse nodes projecting as exceedingly short spines. Ambulacral groove small, V-shaped. Pinnules slender, elongate.

REMARKS. Brachials of most poteriocrinids lack ornament. When present, the ornamentation commonly consists of fine granules or longitudinal or transverse ridges. Thus, the projecting spine-like nodes on the brachials of Poteriocrinid arms indet. #2 are very distinctive. *Chlidonocrinus echinatus*, a Late Carboniferous poteriocrinid from the United States (Strimple & Watkins, 1969), has similar spine-like node ornamentation but only 1 - 2 per brachial and not in an aligned transverse row. The brachials of *Neerkolocrinus typus* have irregular nodose ornament, not aligned in a transverse row and the brachials are much longer. The original illustration from the external mould does not show pinnules, which were not mentioned in the description (Etheridge in Jack & Etheridge, 1892). Without the cup, the specimen is left in open nomenclature.

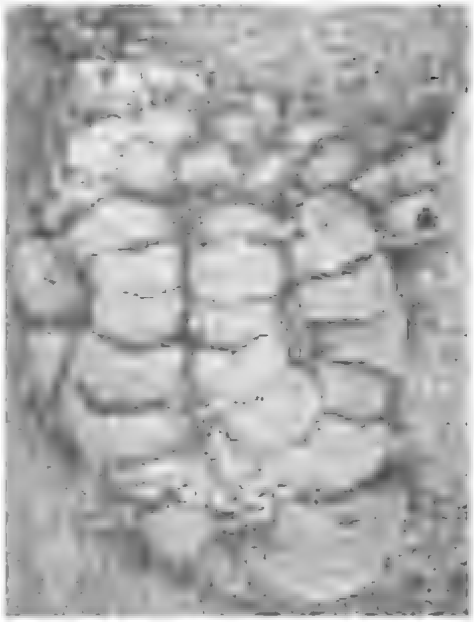


FIG. 21. Taxocrinid indet., lateral view of partial crown QMF38951, ×4.3.

Subclass FLEXIBILIA Zittel, 1895
Order TAXOCRINIDA Springer, 1913
Superfamily TAXOCRINOIDEA Angelin, 1878
Family TAXOCRINIDAE Angelin, 1878

**Taxocrinid** indet.
(Fig. 21)

MATERIAL. QMF38951 from QML508, late Tournaisian, Malchi Formation.

DESCRIPTION. Crown slender, elongate. Cup high truncated cone, with unornamented plates, with apical pits. Basals large, 7.3mm wide, strongly convex transversely with shallow longitudinal medial trough, distally upflared, distal tips incurved. Radials large, 14.0mm long, 14.2mm wide (incomplete), slightly convex longitudinally, strongly convex transversely. Radial facets angustary, with sharply convex outer rim, sloping inward, with short central transverse ridge 1/3 width of facet, with elongate ligament pit and large outer area aboral of ridge; inwardly with transverse pit adjacent to transverse ridge. Anal large, proximal 1/2 in line of radials. Brachials rectilinear, concave or straight longitudinally, strongly convex transversely, deep, not in contact laterally, with faint development of patelloid process, with deep wide V-shaped ambulacral groove. Brachial facets concave, with fine


FIG. 22. A,B, Sagenocrinitoid indet., lateral views of opposite sides of disarticulated crown QMF38952a and b ×2.0.

crenellae and culmina radiating from apex of ambulacral groove to aboral edge of facet covering an arc of 195°. Arms branching at least once and probably several times. Interprimibrachs unknown, but probably present. Anal tube plates large, with crenulate edges. Stem unknown.

REMARKS. QMF38951 is the external mould of both sides of a crushed, disarticulated crown. The specimen is assigned to the Taxocrinidae because the radials are large, upflaring and have angustary radial facets, and the arms were not abutting. It is uncertain whether the cup includes more than 1 anal.

Articular facets of the brachials of *Forbesiocrinus nobilis* de Koninck & Le Hon, 1854 (Springer, 1920, pl. 24, figs 13, 15, 18, 19, 23), *Synerocrinus incurvus* (Trautschold, 1867) (Springer, 1920, pl. 42, figs 8i, 8k) and *Parichthyocrinus nobilis* (Wachsmuth & Springer, 1880) (Springer, 1920, pl. 61, figs 5-8) have narrow crenularia only along the outer edges of the facet. The crenularium of this taxon is quite different, radiating from the growth centre to the outer edges of the ossicle. The specimen probably represents a new genus, but is too incomplete to serve as a holotype.

Order SAGENOCRINIDA Springer, 1913
Superfamily SAGENOCRINITOIDEA Roemer, 1854

**Sagenocrinitoid** indet.
(Fig. 22)

MATERIAL. QMF38952 from QML508, late Tournaisian, Malchi Formation.

DESCRIPTION. Partial set of arms, small. Brachials weakly convex longitudinally, moderately convex transversely; (smooth fine granulate surface reflects grains in matrix). Patelloid process small, weakly developed. Arms branch isotomously twice; 1st branching on 3rd brachial preserved, 2nd branching on 4th brachial of adjacent parts of first branching. Distal part of interbrachial, interprimibrach, or anal series 2

large plates followed by numerous small irregular plates.

REMARKS. This fragmentary specimen may represent parts of 2 rays or part of 1 ray. It is assigned to the Sagenocrinitoidea based on the interprimibrach or interbrachial series and branching pattern of the brachials.

## ACKNOWLEDGEMENTS

Andrew Rozefelds helped collect the Rockhampton Group. Loan of specimens by the curators in charge of collections at the Queensland Geological Survey, Geological Survey of New South Wales, Australian Museum, Australian National University and British Museum is greatly appreciated. Paul Avern processed photographs. GDW extends his appreciation to Washington State University for granting professional leave and to the Director of the Queensland Museum for use of facilites and office space during prosecution of this project. The reviews of Bill Ausich and George Sevastopulo are kindly acknowledged.

## LITERATURE CITED

AUSICH, W.I. & KAMMER, T.W. 1991. Late Osagean and Meramecian *Actinocrinites* (Echinodermata: Crinoidea) from the Mississippian stratotype region. Journal of Paleontology 65: 485-499.

AUSTIN, T. & AUSTIN, T. 1844. A monograph on Recent and fossil Crinoidea, with figures and descriptions of some Recent and fossil allied genera. 3: 33-48, pls 5-6 (London).

BAMBACH, R.K. 1990. Late Palaeozoic provinciality in the marine realm. Geological Society Memoir 12: 307-323.

BASSLER, R.S. & MOODEY, M.W. 1943. Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms. Geological Society of America Special Paper 45: 1-734.

BRANSON, C.C. 1948. Bibliographic index of Permian invertebrates. Geological Society of America Memoir 26: 1-1049.

BROADHEAD, T.W. 1981. Carboniferous camerate crinoid subfamily, Dichocrininae. Palaeontographica. Abteilungen A 176: 81-157.

BROWER, J.C. 1967. The actinocrinitid genera *Abactinocrinus*, *Aacocrinus* and *Blairocrinus*. Journal of Paleontology 41: 675-705.

CAMPBELL, K.S.W. & BEIN, J. 1971. Some Lower Carboniferous crinoids from New South Wales. Journal of Paleontology 45: 419-436.

CAMPBELL, K.S.W. & McKELLAR, R.G. 1969. Eastern Australian Carboniferous invertebrates: sequence and affinities. Pp. 77-119. In Campbell, K.S.W. (ed.), Stratigraphy and palaeontology. (Australian National University Press: Canberra).

DAY, R.W., WHITAKER, W.G., MURRAY, C.G., WILSON, I.H. & GRIMES, K.G. 1982. Queensland geology. Geological Survey of Queensland Publication 383: 1-194.

DUN, W.S. & BENSON, W.N. 1920. The geology and petrology of the Great Serpentine Belt of New South Wales. Part 9 – The geology, palaeontology and petrography of the Currabubula district, with notes on adjacent regions. Section B – Palaeontology. Proceedings of the Linnean Society of New South Wales 45: 337-374, pls 18-24.

DUNSTAN, B. 1898. The Mesozoic Coal Measures of Stanwell and associated formations. Geological Survey of Queensland Publication 131: 1-21.

ETHERIDGE, R. Jr 1892. A monograph of the Carboniferous and Permo-Carboniferous invertebrata of New South Wales. Part II. Echinodermata, Annelida, and Crustacea. Memoirs of the Geological Survey of New South Wales, Palaeontology 5: 65-131, pls 12-22.

GOLDRING, W. 1938. Devonian crinoids from the Mackenzie River Basin (NWT) Canada. Bulletins of American Paleontology 24(81): 1-23.

HALL, J. 1858. Palaeontology of Iowa. Report of the Geological Survey of the State of Iowa 1(2): 473-724.

1861. Descriptions of new species of Crinoidea from the Carboniferous rocks of the Mississippi Valley. Journal of the Boston Society of Natural History 7: 261-328.

JACK, R.L. & ETHERIDGE, R. Jr 1892. The geology and palaeontology of Queensland and New Guinea. (J.C. Beal, Govt Printer: Brisbane).

KAMMER, T.W. & AUSICH W.I. 1992. Advanced cladid crinoids from the Middle Mississippian of the east-central United States: primitive-grade calyces. Journal of Paleontology 66: 461-480.

KONINCK, L.G. de 1877-1878. Recherches sur les Fossiles Paléozoiques de la Nouvelle Galles du Sud (Austrálie). Mémoires de la Société Royale Liège, (1877), ser. 2, Part 1, Texte:1-373; Part 2, atlas, 24 pl., F. Hayez, Bruxelles. Crinoiden: Troisiéne Partie, Fossiles Carboniféres, pp. 158-166, pl. 6 (1878).

1898. Descriptions of the Palaeozoic fossils of New South Wales (Australia): Memoirs of the Geological Survey of New South Wales, Palaeontology 6: 1-298, pls 1-24.

KONINCK, L.G. de & Le HON, H. 1854. Recherches sur les crinoides du terrain carbonifere de la Belgique. Academie Royal de Belgique Memoir 28(3): 1-215.

LANE, N.G. & SEVASTOPULO, G.D. 1987. Stratigraphic distribution of Mississippian camerate crinoid genera from North America and western Europe. Courier Forschunginstitut Senckenberg 98: 199-206.

1990. Biogeography of Lower Carboniferous crinoids. Geological Society Memoir 12: 333-338.

LINDLEY, I.D. 1979. An occurrence of the camerate crinoid genus *Eumorphocrinus* in the Early

Carboniferous of New South Wales. Journal and Proceedings of the Royal Society of New South Wales 112:121-124.

1988. *Glaphyrocrinus*, a new camerate crinoid genus from the Lower Carboniferous of New South Wales. Alcheringa 12:129-136.

LISHMUND, S.R., DAWOOD, A.D. & LANGLEY, W.V. 1985. The limestone deposits of New South Wales. Geological Survey of New South Wales Mineral Resources 25: 1-373.

McKELLAR, R.G. 1966. A revision of the blastoids "*Mesoblastus*? *australis*", "*Granatocrinus*? *wachsmuthii*" and "*Tricoelocrinus*? *carpenteri*" described by Etheridge (1892) from the Carboniferous of Queensland. Memoirs of the Queensland Museum 14: 191-198, pl. 24.

MILLER, S.A. 1889. North American geology and paleontology. (Western Methodist Book Concern: Cincinnati).

1892. North American geology and paleontology, first appendix. (Western Methodist Book Concern: Cincinnati) pp. 665-718.

MILLER, S.A. & GURLEY, W.F.E. 1890. Description of some new genera and species of Echinodermata from the Coal Measures and Subcarboniferous rocks of Indiana, Missouri, and Iowa. Journal of the Cincinnati Society of Natural History 13: 1-25, pls 1-4.

MINATO, M. 1951. On the Lower Carboniferous fossils of the Kitakami Massif, NE Honsyu, Japan. Journal of the Faculty of Science, Hokkaido University ser. 4, 7: 355-382.

MINATO, M., HUNAHASHI, M., WATANABE, J., KATO, M. (eds) 1979. The Abean Orogeny. (Tokai University Press: Tokyo).

MOORE, R.C. & LAUDON, L.R. 1943. Evolution and classification of Paleozoic crinoids. Geological Society of America Special Paper 46: 1-151.

MOORE, R.C. & STRIMPLE, H.L. 1969. Explosive evolutionary differentiation of unique group of Mississippian-Pennsylvanian camerate crinoids (Acrocrinidae). University of Kansas Paleontological Contributions Paper 39: 1-44.

MOORE, R.C. & TEICHERT, K. (eds) 1978. Treatise on invertebrate paleontology. Part T. Echinodermata 2. 3 vols. (Geological Society of America and University of Kansas: Lawrence, Kansas).

PICKETT, J.W. 1960. Note on a Carboniferous crinoid from Swain's Gully, Babbinboon, NSW. The Australian Journal of Science 23: 88.

SHUMARD, B.F. 1858. Description of new fossil Crinoidea from the Palaeozoic rocks of the western and southern portions of the United States. Transactions of the St Louis Academy of Science (1857) 1: 71-80.

SPRINGER, F. 1920. The Crinoidea Flexibilia (2 vols). Smithsonian Institution Publication 2501: 1-486, pls A-C, 1-76.

STRIMPLE, H.L. & KOENIG, J.W. 1956. Mississippian microcrinoids from Oklahoma and New Mexico. Journal of Paleontology 30: 1225-1247.

TERMIER, G. & TERMIER, H. 1950. Paléontologie Marocaine II. Invertébres de l'Erde Primaire. 4. Annélides, Arthropodes, Echinodermes, Conularides et Graptolithes. Service Carte Géologique Morocco, Notes et Mémoires 79(4): 1-279, pls 184-241.

TRAUTSCHOLD, H. 1867. Einige crioideen und andere Thierrests des Jungeren Bergkalks im Bouvernment Moskau. Bulletin de la Societie Imperial Naturalistes de Moscou 15(3-4): 1-49.

WACHSMUTH, C. & SPRINGER, F. 1880. Revision of the Palaeocrinoidea. Part 1. Proceedings of the Academy of Natural Sciences of Philadelphia 1880: 226-378, pls 15-17.

1897. The North American Crinoidea Camerata. Harvard College Museum of Comparative Zoology Memoir 20 (3 vols), 21: 1-897.

WEBSTER, G.D. 1973. Bibliography and index of Paleozoic crinoids, 1942-1968. Geological Society of America Memoir 137: 1-341.

1974. Crinoid pluricolumnal noditaxis pattern. Journal of Paleontology 48: 1283-1288.

1977. Bibliography and index of Paleozoic crinoids, 1969-1973. Geological Society of America Microform Publication 8: 1-235. (3 cards)

1986. Bibliography and index of Paleozoic crinoids, 1974-1980. Geological Society of America Microform Publication 16: 1-405. (5 cards)

1987. Permian crinoids from the type-section of the Callytharra Formation, Callytharra Springs, Western Australia. Alcheringa 11: 95-135.

1988. Bibliography and index of Paleozoic crinoids and coronate echinoderms, 1981-1985. Geological Society of America Microform Publication 18: 1-235. (3 cards)

1993. Bibliography and index of Paleozoic crinoids, 1986-1990. Geological Society of America Microform Publication 25: 1-204. (3 cards)

1997. Lower Carboniferous echinoderms from northern Utah and western Wyoming. Utah Geological Survey Bulletin 128, Paleontology Series 1: 1-65.

WEBSTER, G.D. & JELL, P.A. 1992. Permian echinoderms from Western Australia. Memoirs of the Queensland Museum 32(1): 311-373.

1998. New Permian crinoids from Australia. Memoirs of the Queensland Museum 43(1): 279-339.

WEBSTER, G.D. & LANE, N.G. 1987. Crinoids from the Anchor Limestone (Lower Mississippian) of the Monte Cristo Group southern Nevada. University of Kansas Paleontological Contributions Paper 119: 1-55.

WRIGHT, J. 1932. The Scottish species of *Allagecrinus*. Geological Magazine 69: 337-366, pls 23-25.

1952. The British Carboniferous Crinoidea. Palaeontographical Society Monograph 1(5): 149-190.

1955. The British Carboniferous Crinoidea. Palaeontographical Society Monograph 2(1): 191-254, pls 48-63.

## APPENDIX 1

Locality Register.

GSQ K-21 - Hill behind Pearson's Homestead. 0.8mile N of Old Cannindah road intersection along Cannindah Road, Caswell Creek Group. Collected by R. McKellar.
GSQ K-106 - Along side road off Stanwell-Dalma road. Rockhampton Sheet 1:250,000 yd grid:31760852; Ridgelands 1:100.000 Sheet GR 22024101; Late Carboniferous, Neerkol Formation. Collected by R. McKellar.
GSQL334 - Neerkol Formation, Late Carboniferous, W of Rockhampton.
GSQL3006 - Crow's Nest, NW of Mt Morgan, Mount Morgan 1:100,000 Sheet GR 284854; Gympie Beds of Jack & Etheridge (1892). Collected by J. Smith, 1888.
GSQL3012 - Malchi Creek, probably Malchi Formation, W of Rockhampton, Queensland.
QML508 - Mrs Harding's property, low hills 1km SE of homestead, above limestone hardground. KV252152; 8915 Ridgelands 1:100,000 Sheet, Rockhampton Group. Collected by P.A. Jell & A. Rozefelds.
QML878 - 2000' W of Old Cannindah Homestead, Queensland. Oolitic limestone in Baywulla Formation, Early Carboniferous.
QML1248 - North side of hill behind Old Cannindah homestead, Early Carboniferous Caswell Creek Group, Tournaisian or possibly Visean Tellebang Limestone. 18.0 43.5 Monto 1:100.000 Sheet.

## APPENDIX 2

List of described Carboniferous crinoid taxa from stratigraphic units of Queensland and New South Wales. Taxa preceded by an asterick (*) are not treated systematically herein.

Neerkol Formation, Westphalian, Qld.
- *Denarioacrocrinus neerkolensis* gen. et sp. nov.
- *Denarioacrocrinus? ornatus* sp. nov.
- *Neerkolocrinus typus* gen. et sp. nov
- *Kopriacrinus mckellari* sp. nov.
- *Priminocrinus namoiensis* sp. nov.

Baywulla Formation, Visean, Qld.
- *Litocrinus* sp.

Caswell Creek Group, Visean?, Qld.
- *Aacocrinus* sp. 1
- *Sampsonocrinus cannindahensis* sp. nov.
- *Dialutocrinus?* sp.
- *Platycrinites nux?* (Etheridge, 1892)

Rockhampton Group, Malchi Formation, late Tournaisian, Qld.
- *Actinocrinites* sp. 1
- *Actinocrinites?* sp. 3
- *Aacocrinus* sp. 1
- *Manillacrinus brownei* (Dun & Benson, 1920)
- *Platycrinites* sp. 2
- *Platycrinites* sp. 3
- *Platycrinites* sp. 4
- Camerate indet.
- '*Poteriocrinites'? smithii* (Etheridge, 1892)
- Poteriocrininid cup indet.
- Poteriocrininid arms indet. #1
- Poteriocrininid arms indet. #2
- Taxocrinid indet.
- Sagenocrinitoid indet.

Neil's Creek Clastics, early or middle Tournaisian, Qld.
- *Actinocrinites* sp. 2

Tellebang Limestone, Tournaisian or Visean, Qld.
- *Aacocrinus acylus* sp. nov.

Unknown horizon, possibly Namoi Formation, late Tournaisian, NSW.
- Rhodocrinitid gen. nov.
- *Dichocrinus* cf. *D. laudoni* Broadhead, 1981
- Scytalocrinid? indet.

Namoi Formation, late Tournaisian, NSW.
- **Cribanocrinus biseriatus* Campbell & Bein, 1971
- **Glyphyrocrinus expansus* Lindley, 1988
- *Manillacrinus acanthus* sp. nov.
- *Manillacrinus brownei* (Dun & Benson, 1920)
- *Platycrinites testudo* Campbell & Bein, 1971
- *Platycrinites* sp. 1
- *Holcocrinus barrabaensis* sp. nov.

Goonoo Goonoo Mudstone, late Tournaisian, NSW.
- **Manillacrinus* sp. Campbell & Bein, 1971
- *Platycrinites testudo* Campbell & Bein, 1971
- **Platycrinites* sp. 2 Campbell & Bein, 1971
- *Synbathocrinus ogivalis* de Koninck, 1878
- **Cyathocrinites* sp. Campbell & Bein, 1971

Dangarfield Formation, late Tournaisian, NSW.
- **Eumorphocrinus elongatus* Lindley, 1979
- **Glaphyrocrinus expansus* Lindley, 1988
- **Glaphyrocrinus minutus* Lindley, 1988

Flagstaff Formation?, Visean?, NSW.
- Actinocrinitid indet.

# NEW PERMIAN CRINOIDS FROM AUSTRALIA

GARY D. WEBSTER AND PETER A. JELL

Webster, G.D. & Jell, P.A. 1999 06 30: New Permian crinoids from Australia. *Memoirs of the Queensland Museum* **43**(1): 279-339. Brisbane. ISSN 0079-8835.

New crinoids are described from the Permian of Queensland, New South Wales, Tasmania, and Western Australia. They 1, strengthen affinities with Timor and North America; 2, add to knowledge of biodiversity; 3, improve knowledge of some earlier described taxa; and 4, extend the stratigraphic value of *Neocamptocrinus*.
Range of the Isocrinidae is extended down to the Artinskian, based on *Archaeoisocrinus occiduaustralis* gen. et sp. nov. The new Order Ampelocrinida which is recognised by syzygial brachial pairs in which muscular articulation alternates with cryptosyzygial articulation is assigned to the Articulata and includes the Ampelocrinidae, Corythocrinidae, Calceolispongiidae and Tribrachyocrinidae.
Euspirocrinids are recognised in the Artinskian and possibly Roadian of eastern Australia, extending their range from the Visean. Three flexible crinoids are recognised in the Artinskian of WA.
*Cymbiocrinus cherrabunensis* is designated the type species of the *Metacalceolispongia* gen. nov. Other new genera and species described are *Anaglyptocrinus willinki*, *Necopinocrinus tycherus* and *Eidosocrinus condamnensis*. New species described are *Platycrinites halos*, *Aulskocrinus? bananaensis*, *Neocamptocrinus catherinensis*, *Spaniocrinus geniculatus*, *Glaukosocrinus middalyaensis*, *Pedinocrinus? nodosus*, *Moapacrinus cuneatus* and *Sundacrinus medius*. ❐ *Crinoids, Permian, Queensland, New South Wales, Tasmania, Western Australia.*

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Permian crinoids of Western Australia were reviewed by Webster (1987) and Webster & Jell (1992). Permian crinoids of eastern Australia were reviewed in Webster (1990). Those reviews may be summarised here by noting that the earliest descriptions of Australian crinoids were in 1847, most species have been described since 1949, and that crinoids are widespread in the marginal Permian basins of both eastern and Western Australia.

Paleobiogeography of Australian Permian echinoderms (Webster et al., in press) may be summarised by noting that: 1, Permian echinoderms are common elements in deposits of eastern Australia from Sakmarian into Wordian time and in WA from Sakmarian into Wuchiapingian time; 2, Australian echinoderm faunas are dominated by taxa endemic to Australia and the Tethys, but contain a few taxa found throughout the equatorial belt; 3, Australian faunas show greatest affinity to the faunas of Timor, but contain some North American Carboniferous taxa that are holdovers in Australia or the Tethys; and 4, Australian echinoderms lived in a cooler water, clastic-rich environment of deposition S of 35°S

The purpose of this paper is to: 1, describe new Permian crinoids from Australia; 2, provide new information on some previously described taxa; 3, relate the new material to previously described faunas; and 4, denote the significance of an Early Permian articulate crinoid in WA.

## FAUNAL ANALYSIS

Western Australian crinoids are reported from 5 horizons. This includes previously unreported taxa in 3 horizons, and new information on taxa from the other 2 horizons (Table 2).

The Permian crinoid fauna of the Callytharra Formation is the most diverse in Australia and second largest in the world. Webster & Jell (1992) reported 16 camerates, 37 inadunates, and 1 flexible, increased here to 42 inadunates (6 disparids, 3 cyathocrinids, and 33 poteriocrininids) and 7 flexibles. Most of the new material consists of disarticulated radial plates and fragmentary sets of arms. The 3 species each of *Prophyllocrinus* and *Loxocrinus*, and the arms of a timorechinid show increased affinity of Callytharra and Timor (especially Basleo) faunas. This supports proposed correlation of the Callytharra fauna with part of the Basleo fauna and an Artinskian age for that part of the Basleo faunas (Webster, 1987; Webster & Jell, 1992).

*Glaukosocrinus* in the Callytharra fauna is its first report outside North America, extending the range from the Late Carboniferous into the Permian.

A crown of *Archaeoisocrinus occiduaustralis* gen. et sp. nov., found in the arms of a crown of *Jimbacrinus bostocki*, from the Cundlego Formation on Jimba Jimba Station is the earliest known articulate crinoid. The articulate crinoids were previously known from the Early Triassic to the Recent, thus their range is extended into the Palaeozoic approximately 28 m.y.

The Wandagee Sandstone yielded an abundance of loose columnals of several species of *Calceolispongia*, whereas articulated cups and crowns are rare. No new taxa are described from the Wandagee, but details of *C. abundans* and *C. rubra* suggest that all calceolispongiids: 1, lived either resting on or partly buried within the substrate, with the stem serving as a runner or vestigial tether in the adult stages; 2, had syzygial articulation facilitating differential movement between laterally adjacent 1st and 2nd brachials of each ray; and 3, that together, the 1st and 2nd brachials of all rays formed a facultative tegmen capable of gentle expansion and contraction, as needed for capacity adjustment of the gut tract.

Discovery of an in situ nest and its partly weathered components consisting of several crowns, partial crowns, and fragments of *Neocamptocrinus millyitensis* in the Cherrabun Member of the Hardman Formation provides new information on the arms, and proximal and medial stem of this Wuchiapingian camerate.

Crinoids of eastern Australia are described from 7 stratigraphic units from early Artinskian to Wordian. This includes new taxa from 5 of the units and new information on taxa from 2.

A reconstructed cup and proximal brachials of *Calceolispongia gerthi* from the Sakmarian Berridale Limestone of SE Tasmania has a cylindrical shape that rested on the substrate probably attached by a runner type stem. This supports the interpretation as discussed for *C. abundans* and *C. rubra*.

Pentastellate columnals and disarticulated cup plates of *Nowracrinus ornatus* from the early Artinskian Kansas Beds of NW Tasmania are recognised in the lineage of the early articulate crinoids. Columnals have a crenularium that parallels the stellate outline and nodals have 5 elliptical cirral facets.

*Neocamptocrinus catherinensis* sp. nov. is the first report of the genus from the late Artinskian Catherine Sandstone. *Gissocrinus*? sp. (=*Anaglyptocrinus* sp. herein) was the only crinoid previously reported from the Catherine Sandstone (Willink, 1979b). These two genera are Tethyan and Australian endemics, respectively.

The discovery of *Anaglyptocrinus willinki* in the Wandrawandian Siltstone enlarges that fauna to 12 species in 7 genera. The Wandrawandian Siltstone, with the second largest Permian crinoid fauna in E Australia, contains *Calceolispongia* (3 spp), *Neocamptocrinus* (2 spp), *Notiocatillocrinus* (2 spp) and *Tribrachyocrinus* (2 spp). The Wandrawandian fauna could be referred to as an Australian fauna with Australian endemics *Notiocatillocrinus*, *Nowracrinus*, *Tribrachyocrinus* and *Anaglyptocrinus* and Tethyan endemics *Neocamptocrinus* and *Calceolispongia*; only *Dichocrinus* is found throughout the equatorial belt in the Carboniferous and appears to be a Permian holdover in Australia. *Notiocatillocrinus*, *Neocamptocrinus* and *Calceolispongia* show affinity with the Callytharra Formation and suggest an Artinskian age. The Wandrawandian fauna is in situ, as many specimens retain stem and arms attached and associated brachiopods and corals are in living positions suggesting they lived below storm wave base. Shi & McLoughlin (1997) considered the Wandrawandian Siltstone to represent an offshore environment on an unstable palaeoslope.

For the first time crinoids are reported from the latest Artinskian Condamine Beds of SE Queensland. The Condamine fauna is the most diverse known from E Australia, contains several very large specimens, and is not typical of other Permian faunas of E Australia. It shows affinity with the Basleo faunas of Timor containing *Neocamptocrinus*, *Platycrinites*, *Spaniocrinus*, and *Sundacrinus* in common. It also shows affinity with the Wandagee Sandstone, with *Eoindocrinus praecontignatus* in common, which supports a late Artinskian age for the Condamine Beds. Occurrence of *Calceolispongia* sp. shows affinity with E and W Australian faunas. Other identified elements in the fauna are *Necopinocrinus tycherus* gen. et sp. nov., the youngest known euspirocrinid, and *Moapacrinus cuneatus* sp. nov., perhaps the youngest known cromyocrinid and showing affinity with Artinskian faunas of North America.

Two interesting elements of the Condamine fauna are sets of arms questionably assigned to a stellarocrinid and an indeterminate poteriocrinid. Both have brachials considerably larger than in

most Palaeozoic crinoids. The stellarocrinid(?) arms are unusual, with the pinnules attached to the shorter end and a large protruded node on the longer end of each brachial. Large nodes on the inner side of the brachial are unknown in the crinoids and the pinnules are normally attached to the longer end of the brachial. The nodes would have served as protection for food particles moving along the ambulacral trackway in the wide ambulacral groove in the open feeding posture. Development of the pinnule on the shorter end of the brachial may be a result of enlargement of the longer end to accomodate the prominent node. Brachials of Poteriocrinid indet., arm fragment 1, are the first pseudobiserial reported. They are also bipinnulate and apparently represent a terminal late Palaeozoic evolutionary development.

The Condamine fauna is judged to be near in situ, with several specimens retaining arms and proximal stem. Specimens probably represent storm kills transported a short distance and buried in a silty mud.

*Aatiskocrinus? bananaensis* and a tribrachyocrinid(?) arm fragment from the Wordian Flat Top Formation of central E Queensland are associated with starfish and plant fragments. These are the first crinoids reported from the Flat Top Formation, increase the number of crinoids found in a sandstone matrix and are interpreted as living in a clastic environment.

There are 120 species of Permian crinoids recognised in WA (Teichert, 1949, 1954; Webster, 1987, 1990; Webster & Jell, 1992, herein). However, only 55 (45.8%) are identified species, or referred (cf.) to a named species. All others are referred to generic or higher taxonomic categories and are represented by partial cups or crowns, sets of arms, arm fragments, loose radials, and rarely columnals. In E Australia 60 species of Permian crinoids are recognised (Willink, 1978, 1979a, 1979b, 1980a, 1980b; Webster, 1990; herein). Of these, 49 (81.7%) are identified to, or referred (cf.) to species level. All others are identified like the WA taxa and represented by similar types of incomplete specimens. Among the E and W Australian taxa there are several that merit special comment.

The Dichocrinidae were common in the Early Carboniferous and rare in Late Carboniferous of North America and Europe (Broadhead, 1981; Webster, unpublished compilation). In the Permian they are unknown outside the Tethys, where they are moderately common, especially in Australia. *Neocamptocrinus* is of stratigraphic utility in both E and W Australia although after introduction to Australia lineages may have evolved independently in the two regions. *Neocamptocrinus catherinensis* sp. nov. in the Catherine Sandstone and *N.* sp. in the Condamine Beds increase the stratigraphic utility of the genus. Reports of the stems of *Camptocrinus* (=*Neocamptocrinus*) in Russia (Yakovlev, 1956) and Timor (Wanner, 1924) show the widespread distribution of the genus in the Tethys and suggest its utility for correlation therein.

*Calceolispongia* and *Jimbacrinus* are widespread in the Permian of Australia and the former is known (as *Dinotocrinus*) from Timor (Wanner, 1916, 1924, 1937) and India (Reed, 1928, 1933). Their stratigraphic utility in Australia has been reported by Teichert (1949), Willink (1979b), and Webster & Jell (1992). *Calceolispongia* is considered to have evolved as 2 separate lineages in E and W Australia in the Early Permian (Willink, 1979b; Webster & Jell, 1992).

*Neocamptocrinus* commonly occurs with *Calceolispongia*. These 2 genera had similar, widely tolerant, ecological requirements as reflected in their ability to live in either clastic or carbonate depositional environments. Both taxa were lower level feeders, living attached to runner stems, or in some species of *Calceolispongia* tethered by a dysfunctional stem in the adult stages. When in association, *Calceolispongia* is typically more abundant. *Neocamptocrinus* has a greater stratigraphic range, extending into the Wuchiapingian.

*Platycrinites* (Late Devonian into Late Permian) is one of the few long ranging crinoid genera of the Paleozoic. It also had widely tolerant ecological requirements as it is found in the claystones, marls, and arenaceous limestones of the Callytharra Formation and the mudstones of the Condamine Formation. It is one of the few equatorial genera in the Permian and a higher level trophic feeder.

Euspirocrinids were reported to have a range of Middle Ordovician, Mohawkian, to Early Carboniferous, Tournaisian, by Lane & Moore (in Moore & Teichert, 1978). The discovery of *Anaglyptocrinus willinki* gen. et sp. nov. in the Wandrawandian Siltstone at Warden Head, NSW, and *Necopinocrinus tycherus* gen. et sp. nov. in the Condamine Beds, extends the range of the family into the late Artinskian and possibly early Roadian.

Webster et al. (in press) recognised 37 Permian crinoid genera in Australia. Of these: 34 were

based on cups and crowns and identified to genus; 2 genera were based on stems; and 1 was referred to as Rhenocrinidae n. gen. In this study, 11 genera are reported for the first time from Australia. These are: *Auliskocrinus*?, *Anaglyptocrinus*, *Necopinocrinus*, *Eidosocrinus*, *Archaeoisocrinus*, *Spaniocrinus*, *Glaukosocrinus*, *Pedinocrinus*?, *Sundacrinus*, *Moapacrinus*, *Loxocrinus* and *Prophyllocrinus*. In addition, 9 indeterminate genera, that are probably new for Australia, are based on poorly preserved crowns, cups, sets of arms, arm fragments and loose cup ossicles. Together these bring the total number of Permian crinoid genera for Australia to 56, with *Anaglyptocrinus* replacing *Gissocrinus*? of Willink (1979a). Of the 46 named genera 14 (30.4%) are endemic to Australia, 13 (28.3%) are endemic to the Tethys, 7 (15.2%) are found throughout the equatorial belt, and the other 12 (26.1%) are Permian holdovers in Australia or known from Australia and one other locality outside the Tethys, but at this time, not considered to be cosmopolitan. Bambach (1990) pointed out that there are no true cosmopolitan crinoid taxa in the Permian, since no taxon is found in all four of the biogeographical regions he recognised. Genera referred to as cosmopolitan by Webster et al. (in press) are found throughout the equatorial latitudes and the cooler water higher latitude Australian localities.

Eastern Australian crinoid faunas contain 8 endemic genera whereas WA faunas contain 3. In addition there are 3 Australian endemics common to both. Undoubtedly, there will be additional endemics recognised as more complete specimens of indeterminate taxa are found. These taxa represent evolution in cooler water, clastic-rich environments, not the equatorial belt carbonate rich enviroments typical of most Palaeozoic crinoid faunas. We suggest that the E Australian endemic genera will continue to be a greater number than those of WA. Western Australian taxa currently identified as genus, family, and order indeterminate will probably contain a good percentage of taxa described from Timor. Eastern Australian faunas have less affinity with Timor and evolved in latitudes farther S than those of WA (Webster et al., in press).

## AGES AND CORRELATION

The Permian stratigraphy of Western Australia was correlated internationally on moderately frequent occurrences of ammonoids (Glenister et al., 1993). Few Permian ammonoids have been reported from E Australia so there the regional biostratigraphy is based on brachiopods (Dickins et al., 1964, among others). International correlations of some Permian units of E Australia are not clear (Day et al., 1975).

Eastern and Western Australian crinoid faunas have in common *Dichocrinus*, *Neocamptocrinus*, *Platycrinites*, *Notiocatillocrinus*, *Eoindocrinus*, *Calceolispongia*, and possibly *Jimbacrinus*. Only *E. praecontignatus* is common at species level. The Wandagee Sandstone of WA is late Artinskian (Glenister et al., 1993) and is correlated using *E. praecontignatus* with the Condamine Beds of SE Queensland. An Artinskian age for the Condamine Beds is supported by *Moapacrinus* which is Artinskian in North America (Webster & Lane, 1967).

Occurrence of crinoid genera and species in E and W Australia implies that both regions were connected by seaways in the late Sakmarian to allow the incursion of *Calceolispongia*. In the latest Sakmarian or early Artinskian *Neocamptocrinus* and *Notiocatillocrinus* invaded both areas. In the middle Artinskian *Jimbacrinus* and *Dichocrinus* are common to both regions. *Platycrinites* and *Eoindocrinus praecontignatus* are found in both areas in the late Artinskian. This implies that E and W Australia were interconnected repeatedly in the Early Permian. Because the lineages of *Calceolispongia* and *Neocamptocrinus* are apparently separate in E and W Australia, it would appear that there was a common source for both areas, but not an interconnection for two-way exchange between them.

At the generic and specific level WA faunas correlate most closely with the Basleo faunas of Timor. *Loxocrinus booni*, 2 other species of *Loxocrinus*, and 3 species of *Prophyllocrinus* in the Callytharra Formation support the suggestion (Webster & Jell, 1992) that part of the faunas of the Basleo Beds are of Artinskian age. *Spaniocrinus* and *Sundacrinus* in the Condamine Beds show affinity with the Basleo Beds and support an Artinskian age. All other faunas of E Australia show little affinity with the Basleo Beds, except for the longer ranging, Tethyan endemics *Calceolispongia* and *Neocamptocrinus*.

## STEM ARTICULATA

Discovery of *Archaeoisocrinus* gen.nov. in the Artinskian of Western Australia requires a review of characteristics defining the subclass Articulata. Simms (1988) defined the Articulata on a combination of morphological characters, but most significantly on the absence of the anal

plate in the cup. He pointed out that all of the morphological characters recognised in the Articulata were individually or in various incomplete combinations known in various Palaeozoic taxa, but not in the total combination as found in the post-Palaeozoic articulates.

Simms & Sevastopulo (1993) reviewed the origin of the articulate crinoids, noting that, as defined by Miller (1821), a number of late Palaeozoic crinoids could be included in the Articulata. Furthermore, applying a cladistic study of 9 primitive and derived morphologic characters (Simms & Sevastopulo, 1993, text-fig 2), they compared 3 Middle Triassic articulate genera to 11 Palaeozoic taxa which have been proposed as ancestral, or have close morphological affinities, to the articulates. They also suggested a revised classification of the Palaeozoic crinoids that included major revisions of, as well as supression of the term, Inadunata. We agree with most of the proposed clades of Simms & Sevastopulo (1993), but do not agree, with excluding their middle to late Palaeozoic 'stem-group articulates' from the Articulata. They referred to the post-Palaeozoic Articulata as the 'crown-group articulates'. This makes the Articulata a horizontally defined (Simpson, 1961) taxon. Simms & Sevastopulo (1993) justified the new definition of the Articulata by adding the recognition of the entoneural system enclosed within the thecal plates.

Simms & Sevastopulo (1993) noted several late Palaeozoic crinoids with the entoneural system enclosed within thecal plates. However, all of the Palaeozoic taxa that they discussed had one or more anal plates within the cup, and thus could be excluded from the crown-group articulates or Articulata, following the definition of Simms (1988) in combination with the entoneural system enclosed within thecal plates.

We assert that the synapomorphic feature that defines the Articulata is the development in the arms of syzygial brachial pairs in which muscular articulation alternates with cryptosyzygial ligamentary articulation as illustrated by Willink (1979b, text-fig. 16) for *Meganotocrinus*. We also conclude that brachial morphology described as rectilinear, weakly cuneate, moderately cuneate, strongly cuneate, cuneate biserial and rectilinear biserial may be considered an evolutionary lineage. However, such evolution could and did stop anywhere along this sequence within different crinoid lineages. Thus the 2 states of uniserial (= primitive) and biserial (= derived) arms, as given by Simms & Sevastopulo (1993, text-fig. 2), are insufficient for defining the complex brachial morphology. We agree that biserial arms evolved more than once in the Palaeozoic, once in the Mesozoic, and that they provided greater flexibility of the feeding arm. We also assume that biseriality became a deadend. We suggest that the reason biseriality was a deadend may be that the interior axial canals could not function efficiently in the short zigzag relationship between adjacent brachials in the cuneate and rectilinear biserial conditions, if it ever developed in those forms. Development of the interior axial canals in the cuneate brachials provided greater protection from injury to the canals in the development of muscles at articular facets, at points of arm branching and on the facets of syzygial paired brachials. They were not restricted by short spaces between zigzag facets. Removal of the anal from the cup was an evolutionary trend that was repeated many times throughout the Palaeozoic. The loss of the anals from the cup in the stem-group articulates is considered unrelated to the development of the entoneural system being enclosed in thecal plates, as some genera (*Calceolispongia*, among others) developed an entoneural system enclosed in thecal plates while retaining an anal within the cup.

We agree with Simms & Sevastopulo (1993) that: 1) the Ampelocrinidae and Cymbiocrinidae should be combined and revised; 2) they contain genera that are not stem-group articulates and should not be included within the family; 3) several taxa of stem-group articulates are insufficiently defined to fully evaluate their position in the lineage; 4) Articulata, as here defined, is a monophyletic clade.

We propose that the primitive Articulata possessed the following morphologic features: 1, dicyclic or cryptodicyclic cup; 2, cirri with multiradiate articula distally and transverse ridge articula proximally or cirri with transverse ridge articula throughout; 3, pinnulate arms; 4, brachial articula with ligamentary and clearly defined muscular fossae; 5, first arm division on primibrachs 2-4; 6, entoneural system enclosed in paired canal; 7, syzygial brachial pairs in arms; 8, anals in cup, 1 to 3; and 9, uniserial arms, with cuneate brachials. These morphologic features are found in *Chlidonocrinus*, *Ampelocrinus*, and *Nowracrinus* as shown by Simms & Sevastopulo (1993, text-fig 2), but they included these taxa in their stem-group articulates. It should also be noted that each has a pentagonal stem proximally.

TABLE 1. Comparison of major morphologic characters of genera assigned to the Order Ampelocrinida and isocrinid *Archaeoisocrinus*.

| Family and Genus | Cup Shape | No. Anals | No. IBr | No. Arms | Pinnules/ Ramules | Stem X-sect at cup | Cirrate at cup | Anal Sac | Facet Type |
|---|---|---|---|---|---|---|---|---|---|
| Corythocrinidae | | | | | | | | | |
| *Corythocrinus* | conical | 1 | 3 | 20-30 | pinnulate | round | no | ? | plenary |
| *Araeocrinus* | conical | 3 | 4-5 | 20+ | pinnulate | round | ? | long | plenary |
| *Campbellicrinus* | conical | 1 | 3 | 12 | pinnulate | round | ? | short | plenary |
| Ampelocrinidae | | | | | | | | | |
| *Ampelocrinus* | med bowl | 3 | 2 | 10 | pinnulate | pentag | yes | recurved | plenary |
| *Chlidonocrinus* | med bowl | 1 | 2 | 20 min | pinnulate | pentag | yes | ? | plenary |
| *Cymbiocrinus* | low bowl | 1 | 2 | 10 | pinnulate | pentag or rd | yes | ? | plenary |
| *Halogetocrinus* | low bowl | 1 | 3-4 | 10+ | pinnulate | round | yes | ? | plenary |
| *Moundocrinus* | med bowl | 1 | 2 | 10 | pinnulate | subpentag | ? | short | plenary |
| *Oklahomacrinus* | discoid | 1 | 2 | 10 | pinnulate | subpentag | ? | ? | plenary |
| Calceolispongiidae | | | | | | | | | |
| *Allosocrinus* | med bowl | 1 | - | 5 | pinnulate | subpen to rd | ? | ? | plenary |
| *Calceolispongia* | high bowl | 1 | - | 5 | pinnulate | subpen to rd | yes | ? | plenary |
| *Jimbacrinus* | high bowl | 1 | - | 5 | pinnulate | subpen to rd | no | ? | plenary |
| *Metacalceolispongia* | med bowl | 1 | 2 | 11+? | pinnulate | pentag | ? | ? | plenary |
| Tribrachyocrinidae | | | | | | | | | |
| *Tribrachyocrinus* | globe | 3-4 | 2 | 12 min | ramules | round | no | short | plenary |
| *Meganotocrinus* | globe | 1 | 2 | 20 | ramules | round | no | short | plenary |
| *Nowracrinus* | globe | 1 | 2 | 20 | ramules | round | yes | short | plenary |
| Insertae sedis | | | | | | | | | |
| *Tasmanocrinus* | conical | 0 or 1? | 2 | 6 min | pinnulate | pentag | yes | short | peneplenary |
| Isocrinidae | | | | | | | | | |
| *Archaeoisocrinus* | discoid | 0 | 2 | 10 | pinnulate | pentag | ? | ? | plenary |

We consider *Corythocrinus*, from the late Tournaisian of Indiana (Tables 1, 2), the oldest Articulata. This is followed, in order of earliest occurrence, by *Chlidonocrinus*, *Cymbiocrinus* and *Ampelocrinus*, from the Visean of North America. We consider the report of *Ampelocrinus* from the Visean of England (Wright, 1951) a questionable identification. Offshoots of the Ampelocrinidae include the Calceolispongiidae, a Late Carboniferous–Permian lineage, and Tribrachyocrinidae, a Permian lineage. Thus, our higher level classification is:

Subclass Articulata
Order Ampelocrinida ord. nov.
Order Millericrinida
Order Cyrtocrinida
Order Bourgueticrinida
Order Isocrinida - with *Archaeoisocrinus* gen. nov.
Order Comatulida
Order Uintacrinida
Order Roveacrinida

Origin of the Ampelocrinida is uncertain. Strimple & Watkins (1969) suggested that *Corythocrinus* was derived from a rhenocrinid because the plicate plates of the anal tube indicated affinities between these two forms; however, plicate tube plates are also known in poteriocrinitids and are common among dendrocrinids. Moore & Teichert (1978) considered the Ampelocrinidae derived from the Decadocrinidae, but gave no explicit reasons for supporting this relationship. Because so many stem articulates have 1 anal, we suggest that the Ampelocrinida might be derived from a cyathocrininid, such as *Lecythocrinus*, where the radianal had already been eliminated from the cup, or *Corynecrinus*, where the radianal and anal X are above the posterior basal. However, the 3 anals in *Ampelocrinus* and *Araeocrinus* suggest that the presence of a single anal may not be a primitive character of the group. Carboniferous evolution of the Ampelocrinida occurred in North America and Europe, whereas the Permian record is within the Tethys, especially E Australia, except for North American species of *Halogetocrinus* and *Allosocrinus* (Table 2).

Moore & Jeffords (1968) described several taxa with pentagonal and pentastellate columnals from Devonian and Carboniferous strata of the United States. The cups are either unknown or not recognised in association with the columnals. The geographic distribution of such

TABLE 2. Range chart of genera assigned to the Ampelocrinida. (x) indicates age of type species. (—) indicates age of species assigned to the genus. United States series names used for Carboniferous because known record is restricted to North America.

| | Carboniferous (part) | | | | | | | | Permian (part) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Family & Genus | Osag. | Mrmc. | Chst. | Morw. | Atok. | Dsmn. | Mssr. | Vrgl. | Assl. | Skmr. | Artk. | Road. | Word. | Capt. | Wuch. |
| Corythocrinidae | | | | | | | | | | | | | | | |
| *Corythocrinus* | x | | | | | | | | | | | | | | |
| *Araeocrinus* | | | | | x | | | | | | | | | | |
| *Campbellicrinus* | | | | | | | | | | x | | | | | |
| Ampelocrinidae | | | | | | | | | | | | | | | |
| *Ampelocrinus* | | | x— | — | | | | | | | | | | | |
| *Chlidonocrinus* | | — | x | | | — | | | | | | | | | |
| *Cymbiocrinus* | | x— | — | — | | | | | | | | | | | |
| *Halogetocrinus* | | | | | — | | x | — | — | | | | | | |
| *Moundocrinus* | | | | | — | | x— | — | | | | | | | |
| *Oklahomacrinus* | | | | | — | — | — | x | | | | | | | |
| Calceolispongiidae | | | | | | | | | | | | | | | |
| *Allosocrinus* | | | | | | — | x | — | — | | | | | | |
| *Calceolispongia* | | | | | | | | | | — | x | — | | | |
| *Jimbacrinus* | | | | | | | | | | — | x— | | | | |
| *Metacalceolispongia* | | | | | | | | | | | | | | x | |
| Tribrachyocrinidae | | | | | | | | | | | | | | | |
| *Tribrachyocrinus* | | | | | | | | | | — | x | — | | | |
| *Meganotocrinus* | | | | | | | | | | | —x— | | | | |
| *Nowracrinus* | | | | | | | | | | | —x— | | | | |
| Incertae sedis | | | | | | | | | | | | | | | |
| *Tasmanocrinus* | | | | | | | | | | x | | | | | |

columnals is unknown. We suggest that such forms should be investigated as possible stem articulates.

## SYSTEMATIC PALAEONTOLOGY

Crinoid teminology follows Ubaghs et al. (in Moore & Teichert, 1978), with columnal patterns after Webster (1974). Measurements are given as: length, parallel to the central axis; width, transverse to, but never cutting or joining the central axis; and depth, normal to, and may join the central axis. Curvature of the cup walls, plate circlets within the cup and fixed brachials are referred as: incurved if distally bending toward, vertical if parallel to, weakly to strongly flaring if bending away from and horizontal if perpendicular to the central axis.

Material collected by us came from localities entered in the Queenland Museum Locality Register (QML), and is curated in the Queensland Museum Palaeontological Collection (QMF). Other palaeontological collections referred to are indicated by the following prefixes: Geological Survey of Queensland, Brisbane (GSQ); Geological Survey of Western Australia, Perth (GSWA); Geological Survey of New South Wales, Lidcombe (MM); Department of Geology, University of Queensland, (UQ); The Natural History Museum London (BME); and Tasmanian Museum (TM).

Subclass CAMERATA Wachsmuth & Springer, 1885
Order MONOBATHRIDA Moore & Laudon, 1943
Superfamily HEXACRINITOIDEA Wachsmuth & Springer, 1885
Family DICHOCRINIDAE Miller, 1889
Subfamily DICHOCRININAE Miller, 1889

### **Dichocrinus** Münster, 1839

TYPE SPECIES. *Dichocrinus radiatus* Münster, 1839 from the Early Carboniferous of Belgium; by monotypy.

### **Dichocrinus**? sp.
(Fig.1B)

MATERIAL. GSWAF50172, from GSWAL119377, Billidee Formation, Artinskian.

DESCRIPTION. Crown small, 29.4mm long (incomplete), 25.8mm wide (arms flared). Cup elongate, cylindrical, unornamented. Basal circlet unknown. D radial 7.7mm long, 3.5mm wide (incomplete), gently convex longitudinally and transversely, with narrow shoulders sloping abmedial. Radial facet angustary, rounded aborally. Anal large, 7.4mm long, 4.6mm wide, widest at base, tapering distally, in line with radials. Arms 2 per ray, isotomous branching on 2nd primibrach, biserial above secundibrach 4-7. Brachials cuneate, moderately convex longitudinally, strongly convex transversely. One

slender pinnule per brachial on long side. Stem and tegmen unknown.

REMARKS. This is the first unornamented *Dichocrinus* reported from the Permian of Australia. Several species of *Dichocrinus* from the Early Carboniferous of the United States have a distally tapering anal plate and most have 10 arms (Broadhead, 1981). The 10 arms are a primitive condition in the genus. Lacking the tegmen, the generic assignment is questioned. The Billidee Formation specimen probably represents a new species, but lacking the basal circlet and tegmen, it is left in open nomenclature.

**Auliskocrinus** Broadhead, 1981

TYPE SPECIES. *Dichocrinus crassitestus* White, 1862 from the late Tournaisian upper part of the Burlington Limestone, Iowa; by original designation.

**Auliskocrinus? bananaensis** sp. nov.
(Fig. 1A)

ETYMOLOGY. From Banana in central Queensland.

MATERIAL. HOLOTYPE: QMF38897 from QML806.

DIAGNOSIS. Anal tube large, conical, distally tapering above the posterior interradius; cup truncated cone-shaped; basal circlet very short; brachials rectilinear.

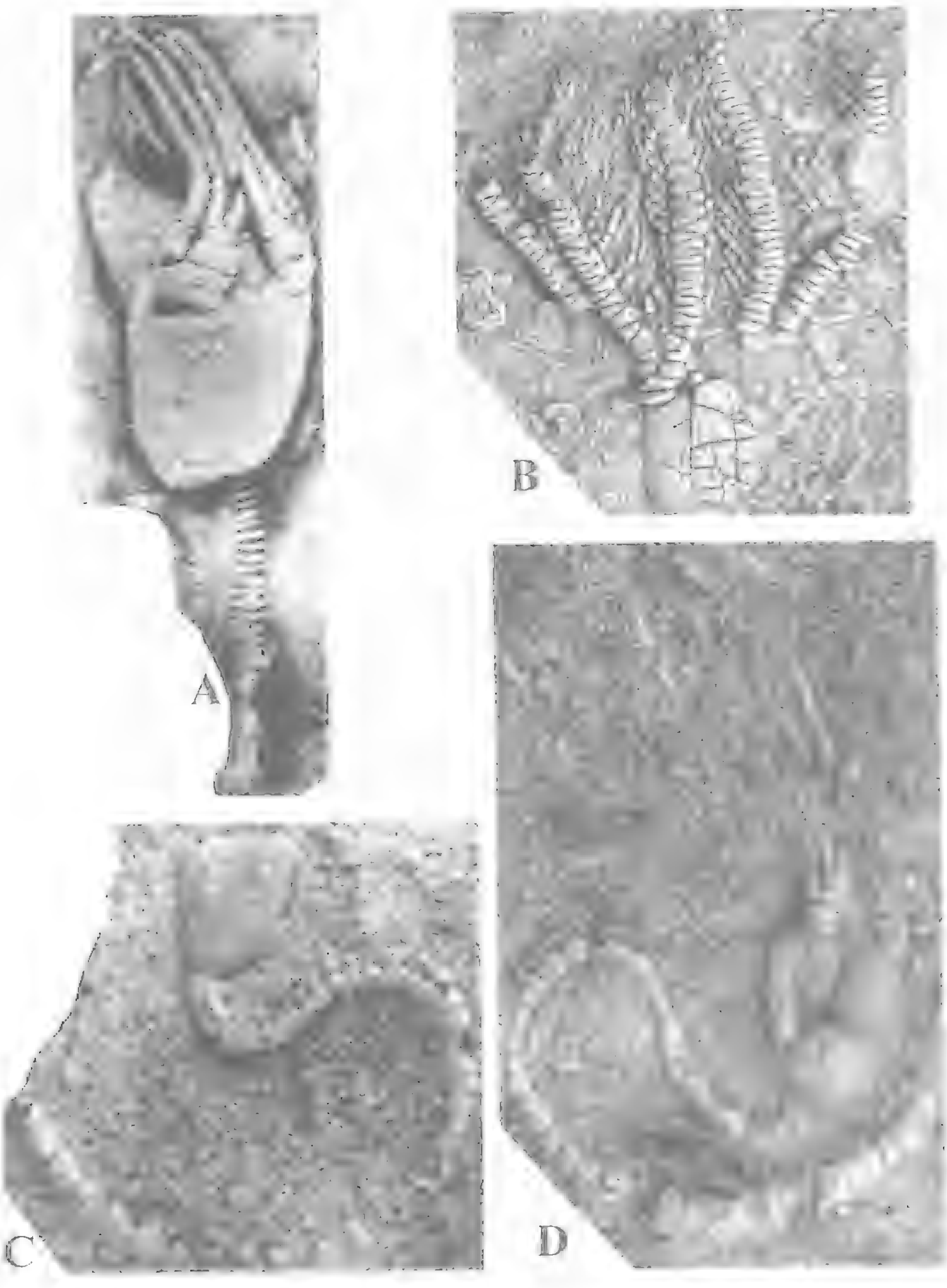
DESCRIPTION. Specimen small, 26.2mm long. Crown small, cylindrical, 16.1mm long, 8.2mm wide at tip of anal tube. Calyx robust, 12mm long to tip of anal tube. Cup truncated conical, 7.4mm long, 6.9mm wide at radial summit; plates smooth; sutures flush. Basal circlet shallow distally flared bowl, 2mm long, 4.8mm wide. Radials large, 5.9mm long, 5mm wide at base of radial notch, longitudinally moderately convex proximally becoming gently convex distally, moderately convex transversely, forming most of cup wall, subvertical distally. Radial facet angustary, 3mm wide, moderately convex projecting from radial aborally. Single anal large, 6mm long, in radial circlet. Tegmen formed of numerous small plates. Anal tube conical, formed of small irregular polygonal plates, tapering distally, distal opening above posterior interradius. Arms relatively short, 11mm long, slender, 4 per ray, isotomously branching on axillary 2nd primibrach. Brachials rectilinear, wider than long, slightly convex longitudinally, strongly convex transversely, with single pinnule on opposite sides of arm. Primibrach 1 much wider (2.6mm) than long (0.7mm). Axillary primibrach 2 3mm wide, 0.8mm long. Stem round, 1.2mm diameter at cup, 10.1mm preserved, heteromorphic. Noditaxis N1; nodals longer and wider than internodals; latus strongly rounded.

REMARKS. *Auliskocrinus? bananaensis* is preserved as an external mould with the C ray centred.

Arguments could be made for erecting a new genus for *A.? bananaensis* or assigning it to *Dichocrinus*. The cup shape, position and plate structure of the anal tube, and rectilinear brachials of *A.? bananaensis* are atypical of the closely related *Auliskocrinus* and *Dichocrinus*. Cup shape of *Auliskocrinus* is relatively high, subconical or slightly globose whereas *Dichocrinus* is relatively high conical. In both genera the basal circlet forms a significant part of the cup wall. Only *D. dichotomus*, an early Visean species with biserial arms, has a bowl-shaped cup with a low upflaring basal circlet, similar to *A.? bananaensis*. No member of the Dichocrininae (Broadhead,1981, fig. 2) has a conical, distally tapering anal tube projecting above the tegmen over the posterior interradius as in *A.? bananaensis*. The small more centrally located vertical anal tube of *Auliskocrinus* is formed of laterally interlocking columns of hexagonal rather than irregular plates, and the genus has slightly cuneate brachials. The tegmen of *Dichocrinus* is typically low, but may be moderately elevated with the anal opening flush or only slightly projected above the tegmen (Broadhead, 1981). Brachials of *Dichocrinus* are either cuneate or biserial, most commonly rectilinear proximally becoming moderately to strongly cuneate distally. Most advanced species have biserial brachials with 20 arms (Broadhead, 1981). With the exception of the truncated conical cup, 20 arms, and projected anal tube, *A.? bananaensis* retains primitive features of *Dichocrinus*.

Variation in cup shape and tegmen structure of monotypic *Auliskocrinus* is unknown (Broadhead, 1981). We assign this specimen to *Auliskocrinus* because the tegmen forms a high cone with a terminal anal opening and the

FIG. 1. A, *Auliskocrinus? bananaensis* sp. nov., C ray view of crown with tegmen, holotype QMF38897, ×4.3. B, *Dichocrinus?* sp., lateral view of partial crown GSWAF50172, ×2.5. C,D, *Neocamptocrinus catherinensis* sp. nov. C, D-E interray view of partial crown, paratype GSQF13487, ×2.5. D, C ray view of crown, holotype GSQF13486, ×2.5.


A
B
C
D

rectilinear brachials are more similar to the slightly cuneate brachials of *Auliskocrinus*.

### Subfamily CAMPTOCRININAE Broadhead, 1981

### **Neocamptocrinus** Willink, 1980

TYPE SPECIES. *Neocamptocrinus bundanoonensis* Willink, 1980a from the Wordian Berry Formation, NSW; by original designation.

REMARKS. Willink (1980a) defined *Neocamptocrinus* primarily on the distinctive inflated tegmen formed of 5 large orals, and numerous small interambulacral and anal plates. He noted *Neocamptocrinus* as a common element in E Australia, recognised 3 species on the basis of cups, another 7 species on columnals, and considered the genus of potential stratigraphic value. In WA there are 3 species (Webster,1990; Webster & Jell,1992), a pluricolumnal from the Callytharra Formation (Webster, 1987) and very large pluricolumnals in the Wandagee Sandstone (Webster & Jell, 1992).Willink (1980a) considered the coiled elliptical stem typical of *Neocamptocrinus*. Broadhead (1981) noted that the elliptical stem distinguishes the Camptocrininae, whereas Dichocrininae have a round stem. Webster (1987) reported stems of *Camptocrinus* cf. *C. indoaustralicus* (considered *Neocamptocrinus* by Webster & Jell, 1992) to vary from slightly elliptical proximally to elliptical to subrectangular distally. Webster & Jell (1992) noted that the proximal stem of *N. millyitensis* is nearly circular in section, becoming elliptical distally. New material of *N. millyitensis* shows the curvature of the enrolled proximal nearly circular part and the transition from that into the strongly elliptical part (Figs 2A-C; 3A,B; 4C,D).

The range of *Neocamptocrinus* in E Australia is from the Sakmarian, Billop Formation of Tasmania, into the Wordian, Condamine Beds of Queensland. In stratigraphic sequence, species recognised are:

*N.* sp. nov., Condamine Beds

*N. bundanooensis* Willink, 1980a, Berry Formation

*N. catherinensis* sp. nov. Catherine Sandstone

*N. wardenensis* Willink, 1980a, Wandrawandian Siltstone

ø*N. tasmaniensis* (Sieverts-Doreck, 1942), Crinoidal Zone

*N. millerensis* Willink, 1980a, Billop Formation

The following columnal (ø) species are considered junior synonyns of ø*N. tasmaniensis*: ø*N.? sievertsae* Willink, 1980a, ø*N.? doreckae* Willink, 1980a, ø*N. bernacchiensis* Willink, 1980a, ø*N.? banksi* Willink, 1980a, and ø*N.?* sp. cf. *N.? tasmaniensis*. These are all from the Crinoidal Zone on Maria Island and represent different parts of the stem of one species.

In general, species of *Neocamptocrinus* are distinguished on cup plate ornamentation, cup plate shape, ornament of tegmen plates, and number of arms. The oldest form known, *N. millerensis*, has a slender high cup with a vermiform ornament, whereas *N. wardenensis* has a lower, more bulbous cup and coarse node and irregular ridge ornament. The plates of *N. catherinensis* sp. nov. are smooth, but the tegmen is a prominent conical projection above the posterior interray. Ornament on *N. bundanoonensis* consists of pits on the cup plates. Cup plates of *N.?* sp. indet. (Willink, 1980a, pl. 4, figs 17-26) probably belong with ø*N. tasmaniensis* from the same stratigraphic unit (Crinoidal Zone). This form would have had a lower cup with a longitudinal trending vermiform ornament.

In WA *Neocamptocrinus* ranges from the late Sakmarian, basal Callytharra Formation, into the Wuchiapingian, Cherrabun Member of the Hardman Formation:

*N. millyitensis* Webster & Jell, 1992, Cherrabun Member

ø*N.* sp. Webster & Jell, 1992, Wandagee Sandstone

*N. occidentalis* Webster, 1990, Cundlego Sandstone

*N. barrabiddyensis* Webster & Jell, 1992, Bulgadoo Shale

ø*N.* sp. Webster, 1987 (as *Camptocrinus* cf. *C. indoaustralicus*), Callytharra Formation

*N. barrabiddyensis* lacks ornamentation, *N. occidentalis* has fine granular ornament on cup plates, and *N. millyitensis* is smooth but has nodes on some oral plates. All have more globose cup shapes than E Australian species. With 8 arms per ray *N. millyitensis* has the greatest number known for the genus. Most species have 4-7 arms per ray, but some rays of *N. millerensis* may have 2. The general trends in evolution of *Neocamptocrinus* in Australia were to: 1, lower the cup by flattening the basal circlet and shortening the length of the radials and primanal; 2, increase the number of arms per ray; and 3, increase in size. Cup and tegmen are smooth or have ornament of

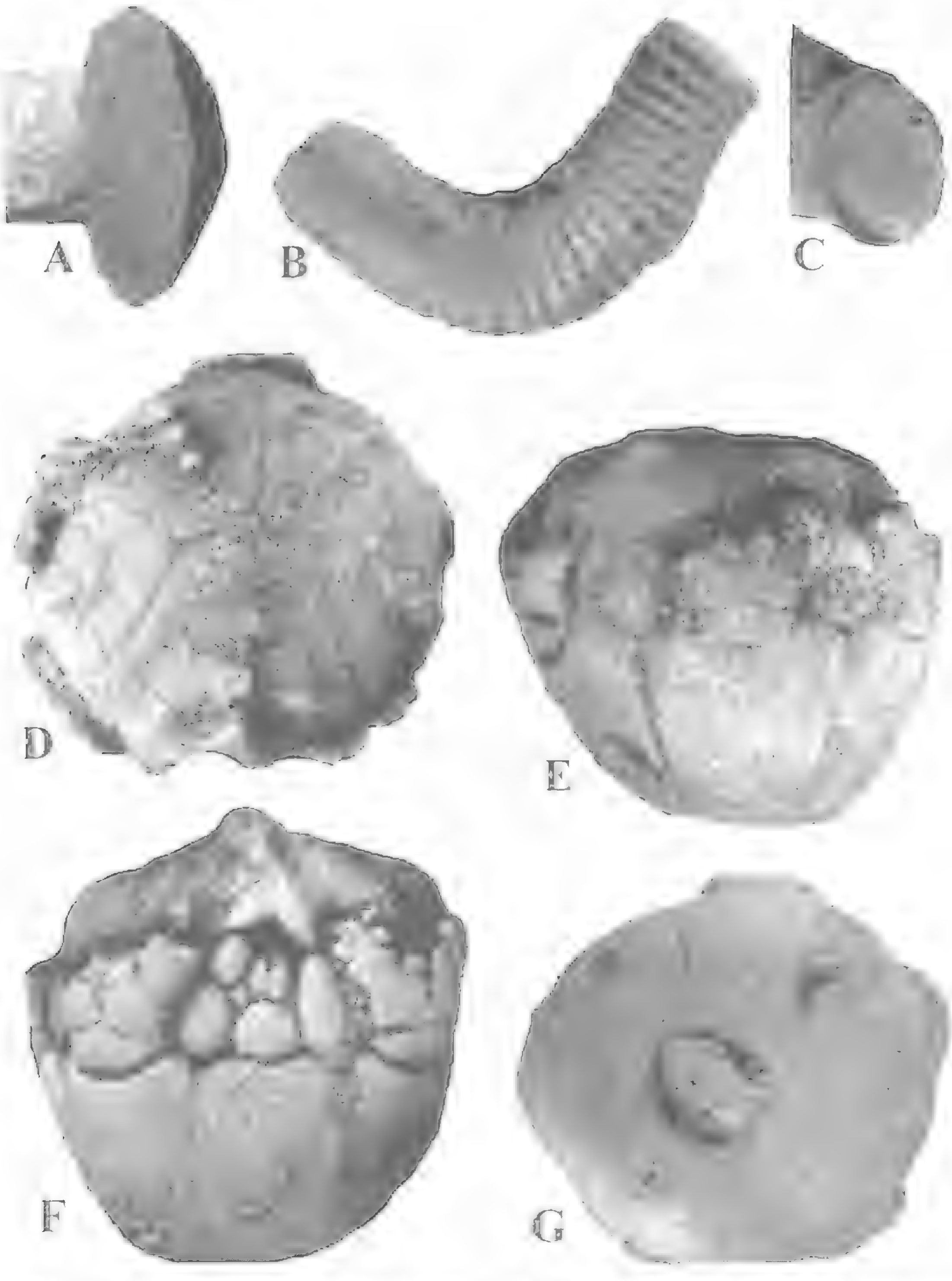



FIG. 2. *Neocamptocrinus millyitensis* Webster & Jell, 1992. A-C, distal facet, lateral stem and proximal facet views of proximal pluricolumnal showing enlargement below theca, QMF38031, ×5. D-G, oral, A ray, posterior and basal views of theca QMF37981, ×2.6.

variable type. *Neocamptocrinus* has the longest stratigraphic range of any Australian Permian crinoid and may have the greatest geographic distribution (columnals referred to as *Camptocrinus* in Timor and Russia are herein considered *Neocamptocrinus*). Only *Calceolispongia* has comparable stratigraphic and palaeogeographic ranges among Australian Permian crinoids.

**Neocamptocrinus catherinensis** sp. nov.
(Fig.1C,D; Table 3)

ETYMOLOGY. From the Catherine Sandstone.

MATERIAL. HOLOTYPE: GSQF13486 from the Guadalupian, Catherine Sandstone, in the upper part of Sandy Creek, Springwood Homestead, Queensland. PARATYPE: GSQF13487, same.

DIAGNOSIS. Cup small to medium sized, high bowl-shaped; tegmen conical projected toward posterior interray; 4 arms per ray.

DESCRIPTION. Crown small to medium sized, cylindrical. Cup high bowl-shaped, plates unornamented. Basal circlet upflared, 2 equal plates, suture in A-CD plane of symmetry, forming basal one third of cup. Radials 5, heptagonal, gently convex longitudinally and transversely, gently flaring proximally, subvertical distally; distal facets with tegmen plates sloping downward gently. Radial facet angustary, nearly 1/2 radial width, gently rounded below distal tips of radial. Anal plate in radial circlet, gently convex longitudinally and transversely. Arms slender, elongate, 4 per ray, branching isotomously on axillary 1st primibrach and 2nd secundibrach. Brachials rectilinear, uniserial proximally, cuneate, becoming biserial distally. Tegmen with rounded conical projection on posterior. Stem nearly circular proximally becoming strongly elliptical distally, heteromorphic in strongly elliptical part; noditaxis $N_{11}$. Nodals formed by fused columnals, with incipient cirral scars on outer side.

REMARKS. The holotype is preserved in the enrolled position as original calcite embedded in fine grained sandstone. The cup is crushed with 2 rays and the anal or edge of a 3rd radial exposed. Proximal parts of the arms show the branching pattern and the distal part of the stem is cirrate. Iron oxide replacement of the plates of the paratype is very soft and partly lost on the enrolled proximal part of the stem and partial crown. The uncrushed cup is smaller than the holotype, the D and E rays are centred, the short anal tube projects on the right and the distal part of the preserved stem is cirrate.

TABLE 3. *Neocamptocrinus catherinensis* sp. nov. measurements (mm). *crushed, +estimated.

| | holotype GSQF13486 | paratype GSQF13487 |
|---|---|---|
| Crown length, incomplete | 26.5 | |
| Calyx length | | 8.5 |
| Cup length | 9.9 | 6.5 |
| Cup width | 10.1* | 5.9 |
| Basal circlet diameter | 4.8 | 3.1 |
| Basal circlet length | 3.2 | 1.2 |
| Radial length | 5.4+ | 4.2 |
| Radial width | 4.4+ | 2.4 |
| First primibrachial length | 1 | |
| First primibrachial width | 2.1 | |
| Proximal columnal diameter | 2.1+ | 1.1 |
| Stem length | 65 | 63.7 |

The tegmen of other species of *Neocamptocrinus* is inflated and may be slightly elevated towards the posterior side, but is not elevated into a conical projection as sharp or prominent as that of *N. catherinensis*. Only *N. wardenensis* with a rounded posteriorly elevated tegmen is comparable. Also the cup of *N. wardenensis* is a lower bowl shape and the basal circlet is shorter and more outflared. The cup of *N. catherinensis* is most similar to that of *N. millerensis*, which has a very low tegmen and relatively longer radials.

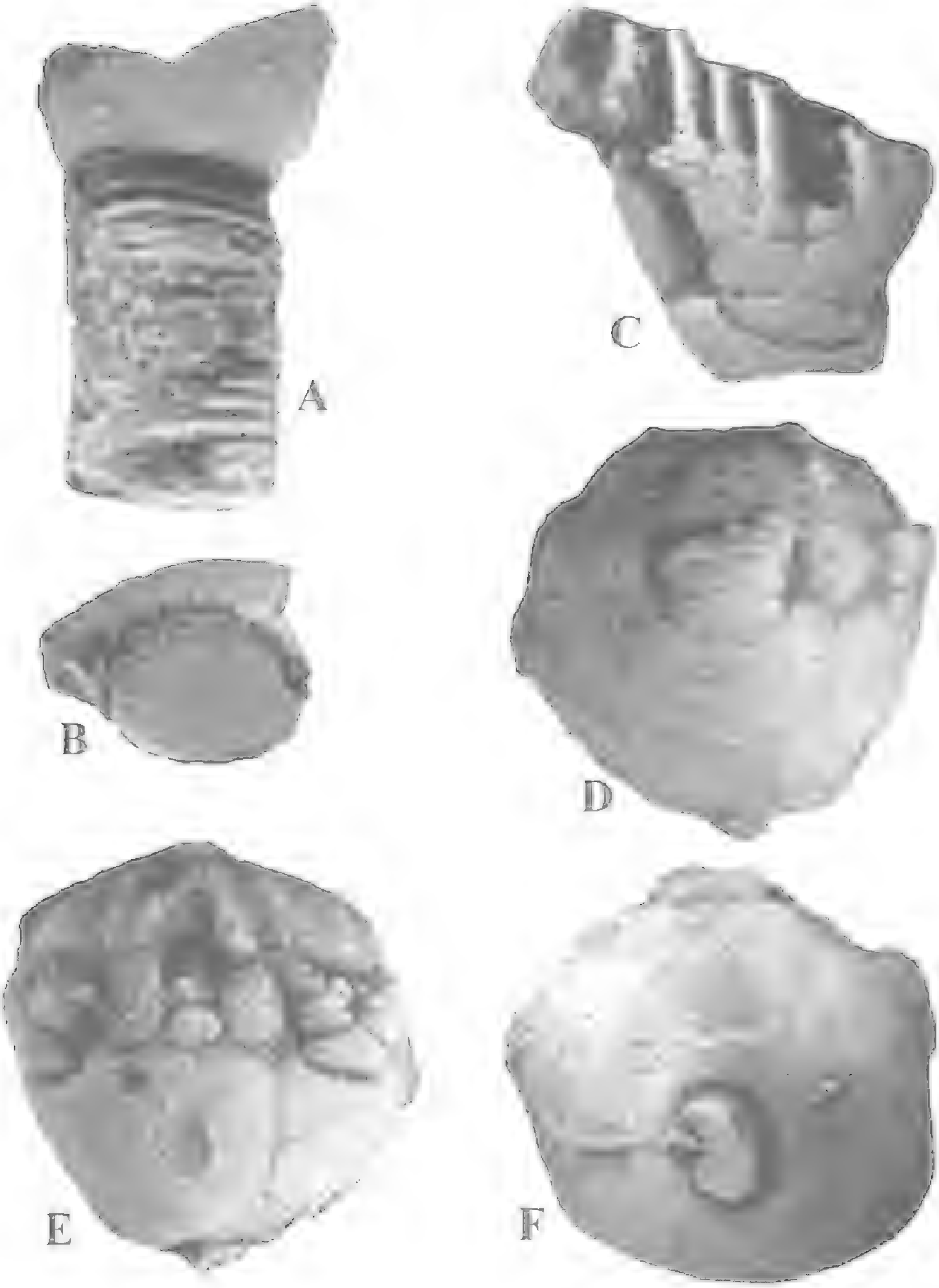
**Neocamptocrinus millyitensis**
Webster & Jell, 1992
(Figs 2-4)

*Neocamptocrinus* sp. nov. Webster,1990: 57, pl. 1, figs 7-11.
*Neocamptocrinus millyitensis* Webster & Jell, 1992: 320, figs 3A-L.

MATERIAL. Crowns QMF37980-F37985, partial calyces (QMF37920, F38986-F38024), partial sets of arms (QMF38025, F38026), radials (QMF37921-F37928), columnals and pluricolumnals (QMF37929-F37971, F38027-F38864), and cirri (QMF37972-F37979, F38865-F38873) from QML772 and 1146).

DESCRIPTION. This description only adds to that of Webster & Jell (1992). Radial facet angustary, approximately half maximum width of radial, sloping outward gently. Brachials cuneate, strongly convex transversely, straight to

FIG. 3. *Neocamptocrinus millyitensis* Webster & Jell, 1992. A,B, lateral and proximal facet views of proximal pluricolumnal and part of basal circlet, QMF38027, ×3.8. C, lateral view of distal end of radial and proximal brachials showing branching pattern, QMF38029, ×4. D-F, A ray, posterior and basal views of theca QMF37980, ×2.6.


A
B
C
D
E
F

slightly convex longitudinally, deep, uniserial proximally, biserial distally. Arms slender, delicate; endotomous branching heterotomous on single primibrach and secundibrach and isotomous on single tertibrach; arms 40, 8 per ray. Brachials with single slender pinnule (up to 9mm long) on long side. Anal series 3-2, with the 2 plates to the left of the anal opening.

Stem elliptical in transverse section; short, more equidimensional (4.6 × 2.4mm) adjacent to cup; becoming longer, flattened and extended elliptical (10.1 × 3.4mm) within 7-8mm, 2-3cm from the cup; becoming less extended elliptical (9.4 × 6.8mm) an unknown distance distally. Noditaxis pattern heteromorphic, with nodals separated by 2 internodals normally, but varying from 1-3. Cirri attach at ends of ellipse, 2 per nodal; cirral facet extending laterally onto 2 adjacent columnals with growth. Cirri not developed in proximal more equidimensional part of stem.

REMARKS. The revised description is based upon new material listed above. Five of the calyces were in situ in a nest with the broken stem segments in the surrounding matrix. Many of the pluricolumnals are coiled, indicating specimens were enrolled prior to fracturing and disaggregation from compaction and weathering. The calyces and pluricolumnals were encased in a clay to silt and fine sand matrix, rather than the typical fine to medium sand of the Cherrabun Member. This suggests that when enrolled, the cirri formed a protective screen around the crown shielding it from the coarser grained sediments. As burial proceeded, finer grained sediments infiltrated the cirri entombing the crowns. Compaction after burial distorted and fractured some of the calyces and broke the stem into pluricolumnals. Modern weathering left a lag gravel of columnals, pluricolumnals, partial and complete calyces, and arm fragments over 3 $m^2$ on a very gently sloping surface. Five complete and 7 partial calyces and numerous stem segments were recovered in situ by excavation to 20cm beneath the lag gravel in the weathered zone.

The arms are delicate, quite slender and, based on a partial set of arms lacking all parts of the calyx, extended a minimum of 25cm above the tegmen. Although uniserial proximally, they become biserial in the middle and distal parts of the arm.

**Neocamptocrinus** sp. nov.
(Fig. 5A-C)

MATERIAL. QMF38900, part of exterior side of 2 rays of partial set of arms, QMF39006, part of interior side of 3 rays of partial set of arms, and QMF39007, pluricolumnal, from QML518.

DESCRIPTION. Axillary primibrach triangular, lateral ends nearly overlap 1st primibrach. Second secundibrach axillary. Brachials strongly convex transversely, straight longitudinally, very deep, cuneate, becoming biserial on the 8th tertibrach, rectilinear biserial on 11th tertibrach. Fine granular ornament on primibrachs and secundibrachs, smooth thereafter. Ambulacral groove narrow, deep V-shaped. Arms 20, 4 per ray, slender, very elongate, 65.8mm (incomplete). Pinnules slender, narrow, one per brachial.

REMARKS. Preservation of both specimens is moderately good, with some parts poorly preserved through oxidation by weathering. The arm branching is typical of *Dichocrinus* or *Neocamptocrinus* with 4 arms per ray. Arms are very delicate and larger than most dichocrinids. They are assigned to *Neocamptocrinus* based on the shape of the brachials, uniserial to biserial arm development, arm branching pattern, and pluricolumnals and columnals of *Neocamptocrinus* in the same interval of the Condamine Beds.

**Neocamptocrinus**? sp.
(Fig. 5D)

MATERIAL. QMF38880 from QML1237.

REMARKS. The partial set of arms is 20.1mm long, 9.4mm wide, and consists of parts of 14 arms. They are assigned to *Neocamptocrinus* because they closely resemble the arms of *N. millyitensis*, as the cuneate brachials are small, biserial, strongly rounded transversely, and bear small delicate pinnules. Webster (1987) reported pluricolumnals of *Camptocrinus* cf. *indoaustralicus* from the type section of the Callythara Formation. Although no cup or calyx has been recovered from the Callytharra Formation, these columnals are now considered to belong to *Neocamptocrinus*, because they are similar to those reported from several stratigraphic units in WA.

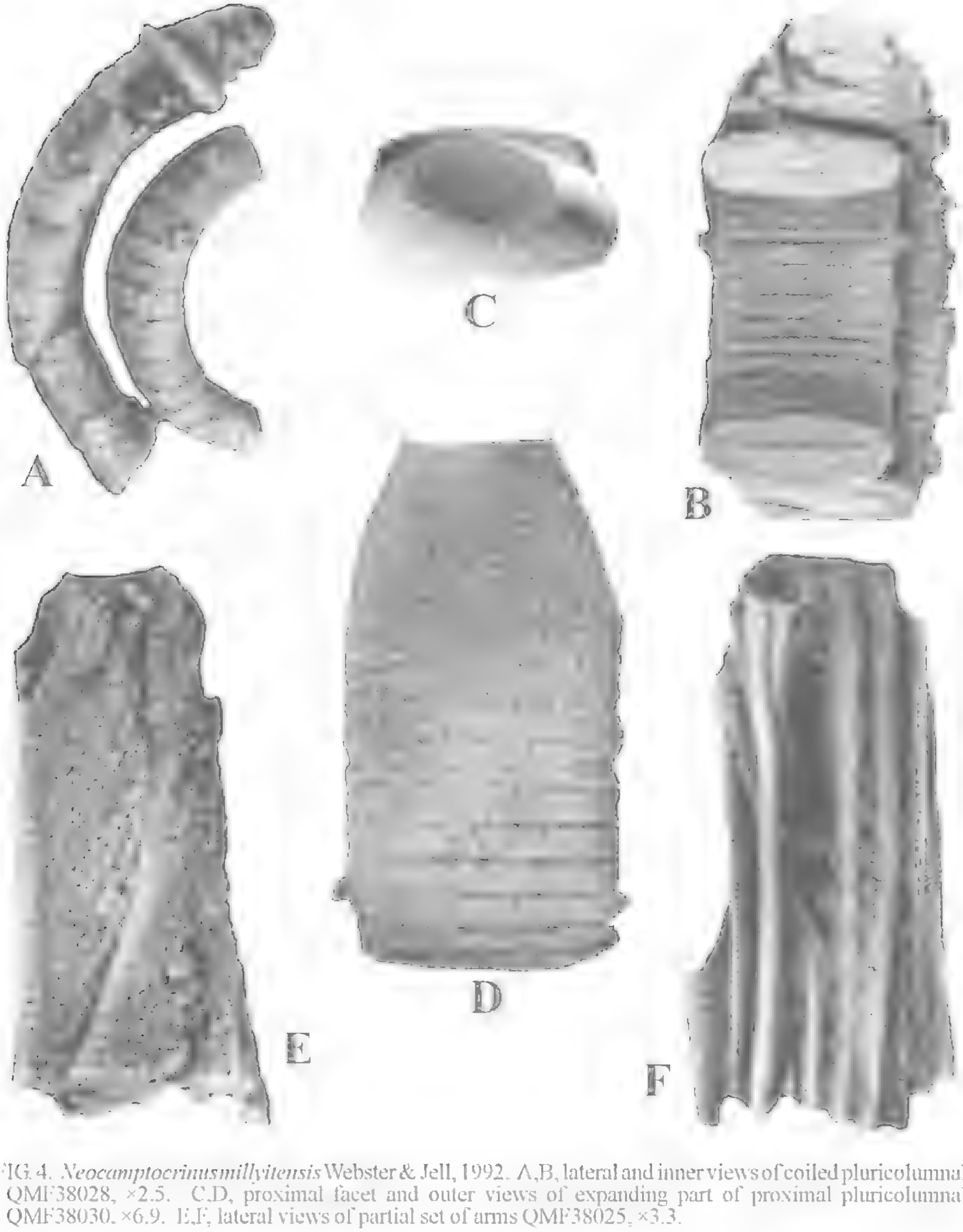
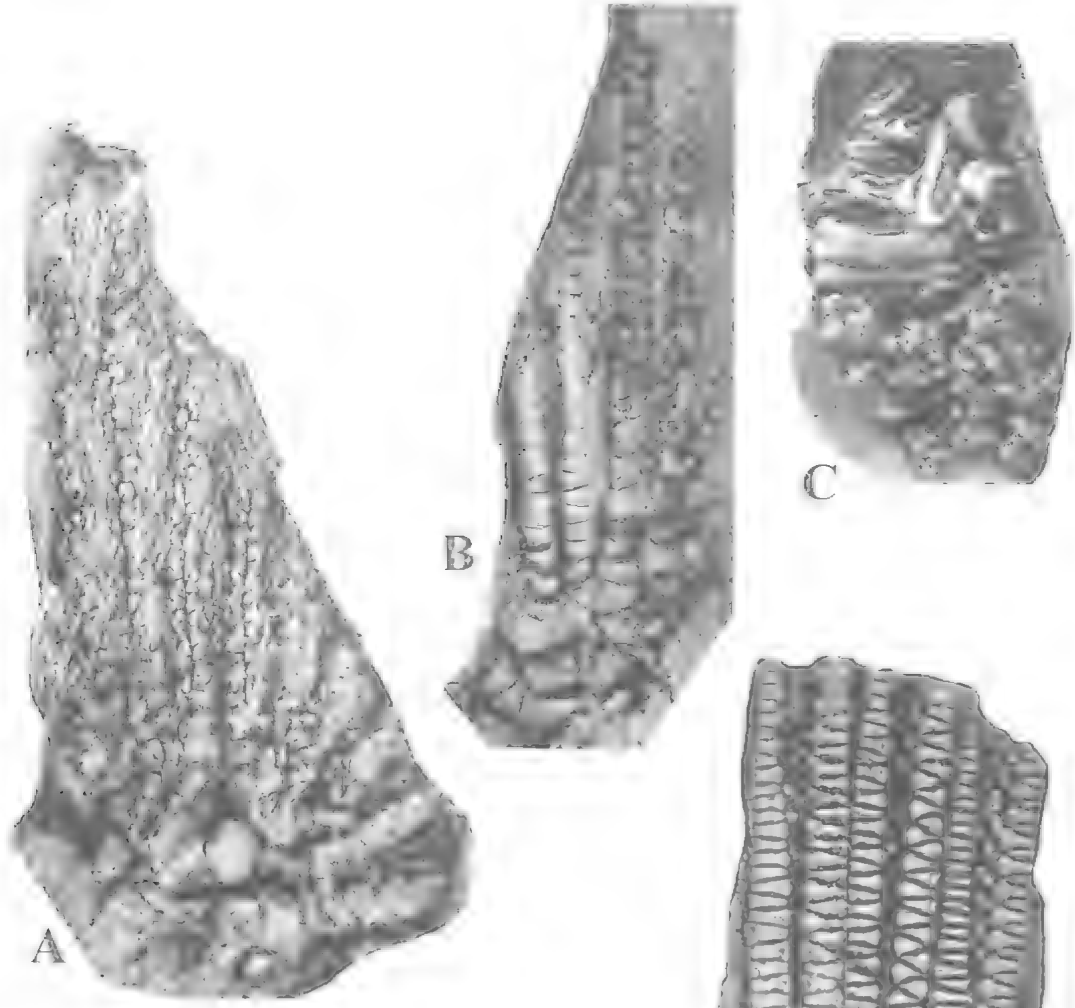


FIG. 4. *Neocamptocrinus millyitensis* Webster & Jell, 1992. A,B, lateral and inner views of coiled pluricolumnal QMF38028, ×2.5. C,D, proximal facet and outer views of expanding part of proximal pluricolumnal QMF38030, ×6.9. E,F, lateral views of partial set of arms QMF38025, ×3.3.



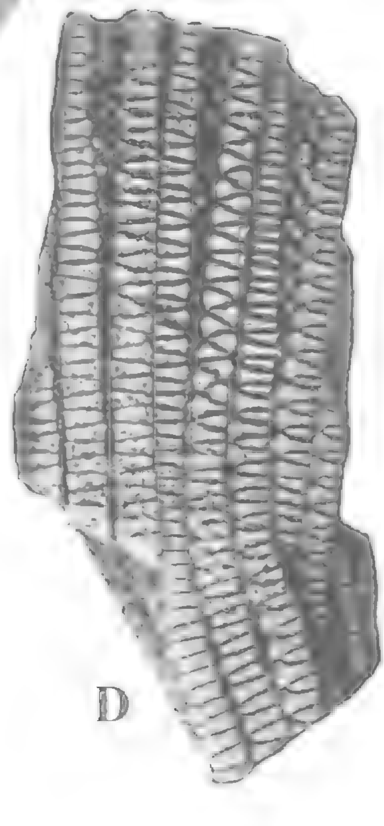


FIG. 5. A-C, *Neocamptocrinus* sp. nov. A, view of interior side of 3 rays of partial set of arms QMF39006, ×1.6. B, lateral view of exterior side of 2 rays of partial set of arms QMF38900, ×1.6. C, lateral view of pluricolumnal QMF39007, ×2. D, *Neocamptocrinus*? sp., lateral view of partial set of arms QMF38880, ×5.1.

Superfamily PLATYCRINITOIDEA
Austin & Austin, 1842
Family PLATYCRINITIDAE
Austin & Austin, 1842

**Platycrinites** Miller, 1821

TYPE SPECIES. *Platycrinites laevis* Miller, 1821 from the early Carboniferous of England, by subsequent designation of Meek & Worthen, 1865.

**Platycrinites halos** sp. nov.
(Fig. 6C,D)

ETYMOLOGY. Greek *halos*, a circle around the sun: refers to the elevated platform around the radial facet.

MATERIAL. Holotype, internal mould with part of proximal tegmen and external mould of basal circlet, 2 radials, and 1 interambulacral, QMF39008 from QML518.

DIAGNOSIS. Cup very large, bowl-shaped; radial facets concave, elliptical, subvertical; arms projecting horizontally away from cup; radial facets large, elliptical, on slightly projecting platforms.

DESCRIPTION. Cup large bowl-shaped, c. 25mm long, estimated 51mm wide, granular texture. Basal circlet large, 14.5mm long, 25mm wide. Basals 3, azygous half size 2 zygous, down widely flaring proximally beneath stem facet, upward widely flaring distally, forming proximal part of cup wall. Radials 5, large, 27mm long, estimated 27mm wide, moderately convex longitudinally, strongly convex transversely, distally shoulders incurved partly around angustary radial facet. Radial facet large, estimated 12.5mm long and wide, concave, elliptical outline, surrounded by narrow platform with sloping rim. Tegmen arched, unknown length. First interambulacral plates very large, estimated 12mm long, 15.7mm wide, laterally flanked by series of small plates covering ambulacral trackways. Stem facet large, estimated 14 ×10mm, separated from cup wall by narrow groove.

REMARKS. This is one of the very large calyx type *Platycrinites*. The arms proximally project horizontally away from the cup. The basal circlet forms a small part of the cup walls as it flares outward much more than upward. The radials are the main part of the cup wall, subvertical proximally and incurved distally. A disarticulated associated columnal beside the base of the cup is 3.2mm long and 18.6mm by an estimated 8mm in transverse section; latus moderately concave; fulcral ridge elevated well above adjacent pits. It is one of the straight columnals of the segmented twist type of Webster (1997) and probably from the same specimen as the cup. The size of the radials is close to that of *Platycrinites* sp. of Webster & Lane (1967) from the Artinskian part of the Bird Spring Formation of southern Nevada. However, no other species of *Platycrinites* has the elevated or rimmed radial facets like *P. halos*.

**Platycrinitid** indet. (columnals)
(Fig. 6A,B)

MATERIAL. QMF38899, 39009, 39010 from QML518.

REMARKS. Elliptical columnals belonging to a platycrinitid, such as *Platycrinites*, *Neoplatycrinus*, or *Stomiocrinus* are of the segmented twist type (Webster, 1997). The facets bear a dual transverse ridge divided by a shallow groove along the long axis. They have an axial canal and 2 or 3 coarse crenulae and culmina on the distal ends of the long axis. Straight and twist columnals are present. They are mentioned to show crinoid diversity in the Condamine Beds.

Subclass CLADIDA Moore & Laudon, 1943
Superfamily CYATHOCRINITOIDEA
Bassler, 1938
Family EUSPIROCRINIDAE Bather, 1890

**Anaglyptocrinus** gen. nov.

TYPE SPECIES. *Anaglyptocrinus willinki*, late Artinskian Wandrawandian Siltstone at Warden Head, NSW.

ETYMOLOGY. Greek *anaglyptos*, wrought in relief, and *krinon*, lily; refers to the low relief, weathered out condition of the holotype.

DIAGNOSIS. Cup medium bowl, with nodose ornament, with shallow apical impressions; infrabasal circlet flat to gently upflared; radial facet angustary, wide radial notches; single large anal above posterior basal; brachials rectilinear, strongly convex transversely, with 4 rows of cover plates above V-shaped ambulacral groove; arms branching isotomously on 4th primibrach and once or twice more; brachials with very small internal axial canal, brachial facets trifacial; anal tube narrow, elongate; stem round, with round lumen.

REMARKS. *Anaglyptocrinus* is distinguished from all other euspirocrinids by the flat to very low basal circlet, medium bowl-shaped cup, and the single anal plate. Cup shape is most similar to but shorter than *Euspirocrinus*. Other taxa assigned to *Anaglyptocrinus* are *Gissocrinus*? *voiseyi* Willink, 1979 and *Gissocrinus*? sp. Willink, 1979.

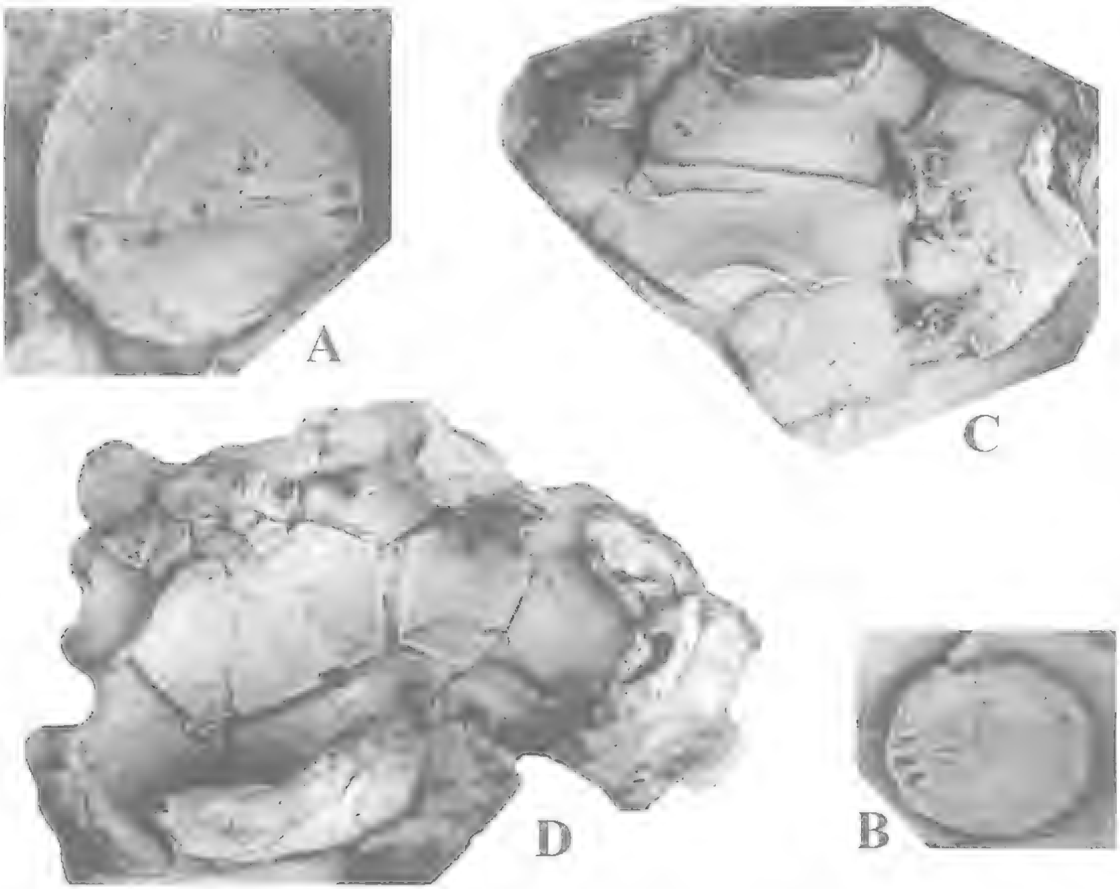



FIG. 6. A,B, Platycrinitid indet. columnals. A, facetal view of twist columnal QMF38899, ×3.6. B, facetal view of weathered straight columnal QMF39009, ×3.8. C,D, *Platycrinites halos* sp. nov., external (×1.5) and internal (×1.3) views of slightly disarticulated and distorted partial theca, holotype QMF39008.

**Anaglyptocrinus willinki** sp. nov.
(Fig.7)

ETYMOLOGY. For R. Willink in recognition of his studies of the Permian crinoids of eastern Australia.

MATERIAL. HOLOTYPE: QMF38913 from QML859.

DIAGNOSIS. As for genus, cup ornament nodose.

DESCRIPTION. Crown slender, elongate, 20.8mm preserved. Cup medium bowl-shaped, nodose ornament on all cup plates, double row of nodes on proximal edge of radial parallel to basal-radial sutures, shallow impressions at junction of basals and radials. Infrabasal circlet flat to widely flaring, barely visible in lateral view. Basals 5, large, 4mm long (incomplete), 5.6mm wide, moderately convex longitudinally and transversely, incurved proximally, subvertical distally, forming lower half of cup wall. Radials 5, 4.4mm long, 5.7mm wide, straight longitudinally below facet, convex longitudinally adjacent to facet, moderately convex transversely. Radial facet narrow, strongly convex outer edge, flaring inwardly to merge with radial shoulders, inner edge smooth with wide concave ambulacral notch, declivate; transverse ridge prominent, divided by gap in middle, dividing facet into inner and outer halves; outer half with small 4-lobed elevation off centre, slightly aboral to gap in transverse ridge; outer fossa divided by low rise from 4-lobed elevation into 2 shallow transversely elongate parts, deepest central aboral; inner fossa transversely elongate, shallow. Radial notches wide. Single anal large, pentagonal, projecting slightly above radial summit, proximally abutting terminated end of CD basal, distally adjoining 2 proximal tube plates. Arms slender, branching isotomously on 4th primibrach and 4th or 5th secundibrach; more distal branching

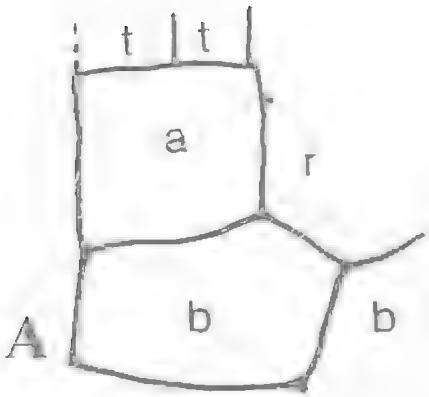



FIG. 7. *Anaglyptocrinus willinki* gen. et sp. nov. A. camera lucida sketch of posterior (×6). B. A ray (×2.8) view. QMF38913. t = tegmen plates, a = anal X, r = C ray radial and b = CD (left) and BC (right) basals.


unknown. Brachials straight longitudinally, strongly convex transversely, deep, with wide V-shaped ambulacral groove. Brachial facets trifacial: transverse ridge wide V, apex pointed adoral, with small single axial canal in slightly elevated centre. Ambulacral cover plates small, 0.05mm long and wide, polygonal, interlocking with adjacent plates longitudinally and laterally; 4 across ambulacral groove, merging with small polygonal plates of tegmen proximally. Anal tube slender, elongate, of 10-11 vertical rows of smooth, laterally interlocking hexagonal plates, 2mm wide, 1.8mm long. Column heteromorphic; noditaxis pattern N3231323. Columnals, round transversely; latus moderately to strongly convex on nodals and internodals; nodals cirrate throughout 21mm of preserved column. Axial canal round.

REMARKS. The crown is crushed with distal parts of the arms and tegmen lost to weathering and the infrabasals and anals are not exposed. Excavation of the under side exposed the C radial, BC and CD basals, parts of the infrabasal circlet, primanal and proximal parts of 2 tube plates (Fig.7A). Ornamentation of the cup was lost or very faintly preserved on parts of the exposed cup, but well-developed on the excavated cup plates.

Willink (1979a) described *A. voiseyi* and *A.* sp. from the Cataract River Formation and Catherine Sandstone, respectively. These forms show similarity of the cup shape and arm branching pattern to the Wandrawandian specimen. They differ from the nodose ornamented cup of *A. willinki* by *A. voiseyi* being ornamented with nodes and sharp ridges on all cup plates as well as the brachials and *A.* sp. bearing prominent interconnected plate ridges on the cup and proximal and distal expanded rims on the brachials giving them an hourglass shape. Thus, the 3 forms make a series from simple nodose ornament to highly ornate, with the simple nodose form the oldest (late Artinskian) and the 2 younger more ornamented forms of approximately the same age (Roadian). Ray ridge and interconnected ray ornament in the crinoids is common in the actinocrinitids, primitive poteriocrinitoids, and a few flexibles. It is not as common in the late Palaeozoic as in the early and middle Palaeozoic. Thus, the ray ridge ornament of the younger forms is considered heterochronous homeomorphy.

Willink (1979a) considered *Glossocrinus* in need of revision, noting that the diagnosis provided by Moore & Teichert (1978) was narrower than that of Angelin (1878) or Bather (1893). Furthermore, he suggested that the Australian forms probably represented the end members of a conservative stock of the

cyathocrinitids that was most closely allied to the Silurian *Gissocrinus*. However, he also suggested the possibility, that the Australian specimens represented heterochronous homeomorphy. The first branching of the arms of *Gissocrinus* is on the single primibrach and the cup is a low bowl, both advanced evolutionary features for this Silurian taxon. By comparison, the type species of *Cyathocrinites*, an Early Carboniferous taxon, has a medium bowl cup and the first branching of the arms is on the 3rd primibrach, both more primitive features. *A. willinki* has even more primitive arm branching than *Cyathocrinites*, but a slightly more advanced cup form. The primitive arm branching with ambulacral cover plates suggests evolution from an unknown conservative stock of the cyathocrininids. The trifacial articulation facets of the brachials and internal dual axial canals are advanced features found in some of the stem articulate crinoids (Simms & Sevastopulo, 1993).

### **Necopinocrinus** gen. nov.

TYPE SPECIES. *Necopinocrinus tycherus* sp. nov. from the Condamine Beds, Elbow Valley area, near Warwick, SE Queensland.

ETYMOLOGY. Latin *necopinus*, unexpected, and *crinon*, lily; refers to a euspirocrinid not being expected to occur in the Permian.

DIAGNOSIS. Cup expanded low bowl, with constricted base, with incurved radial, with coarse nodose ornament on all cup plates; 3 infrabasals, small infrabasal in C ray; radial facets angustary, 1/3 radial width, horseshoe-shaped; 3 small anals above posterior basal; single primibrach axillary. Arms widely spread, branching isotomously. Brachials cuneate; stem round transversely.

REMARKS. The expanded low bowl-shaped cup and axillary 1st primibrach are the 2 most distinctive charaters of *Necopinocrinus*. The cup is most similar to, but more bowl-shaped, than the low cone-shaped cup of *Vasocrinus*.

### **Necopinocrinus tycherus** sp. nov.
(Fig. 8)

ETYMOLOGY. Greek *tyche*, luck or chance, and refers to the Lucky Valley Creek wherein the specimen was found.

MATERIAL. HOLOTYPE: QMF38901, from QML518.

DIAGNOSIS. As for genus.

DESCRIPTION. Cup expanded, low bowl, with constricted flat base, 15mm long, 39mm wide (crushed, compacted in part); all cup plates with coarse nodes, some grading into very short ridges. Infrabasal circlet large, with large circular stem facet, constricted subvertical above stem facet, expanding upflaring distally, divided into 3 plates, 2 large equal plates and 1 smaller plate in C ray, visible in lateral view. Basals large, upflaring, gently convex longitudinally and transversely, forming major part of cup; D-E basal 12mm long (estimated), 20mm wide. Posterior basal 14.8mm long, 10.4mm wide, truncated distally by 3 small facets for anals. Radials large, 12mm long, 18.4mm wide, strongly convex longitudinally, moderately convex transversely, strongly incurved distally to near subhorizontal. Radial facet angustary, horseshoe-shaped, 7.4mm wide, deep, subhorizontal. Three anals small, in line of radials, probably projected slightly above radial facet. Anal tube not preserved. Single primibrach axillary, 5.2mm long, 5.2mm wide, straight longitudinally, strongly convex transversely; distal facets wide spread, separated by narrow concave trough. Secundibrachs wider than long, weakly cuneate, straight longitudinally, strongly convex transversely. Primibrachs and proximal 2 secundibrachs with coarse nodes, with line of coarser nodes along lateral edges. Stem large, circular in transverse section, 9mm diameter.

REMARKS. The crown of *Necopinocrinus tycherus* is crushed along the A-CD plane of symmetry. Radials are cracked and impacted downward, overlapping the distal tips of the basals, the E-A basal is inset and edges are overlapped by adjacent plates, the infrabasal circlet is compressed, brachials are slightly offset from the cup and one another, and the stem and distal parts of the crown are lost.

This specimen represents a conservative stock of the Euspirocrinidae showing an advanced condition of: 1, the anals restricted to the area above the extended posterior basal; 2, the infrabasal circlet of 3 plates; and 3, the arms branching on the single primibrach. *Anaglyptocrinus* and *Necopinocrinus* are the first post Carboniferous euspirocrinids reported, extending the range of the family into the Late Permian.

### Superfamily SCYTALOCRINOIDEA
### Moore & Laudon, 1943
### Family SPANIOCRINIDAE
### Moore & Laudon, 1943

### **Spaniocrinus** Wanner, 1924

TYPE SPECIES. *Spaniocrinus validus* Wanner, 1924 from the Permian Basleo Beds of Timor; by original designation.

FIG. 8. *Necopinocrinus tycherus* gen. et sp. nov., D-E interray view of partial crown QMF38901, ×1.7.

**Spaniocrinus geniculatus** sp. nov. (Fig. 9)

ETYMOLOGY. Latin *geniculatus*, like the bent knee; refers to the knee-shaped brachials.

MATERIAL. HOLOTYPE: QMF38987 from QML518. PARATYPE: QMF39011, same.

DIAGNOSIS. Crown slender, elongate; cup medium bowl; ornament of coarse nodose to short irregular ridges continuing onto brachials, with prominent longitudinal ridge or keel along middle of brachials; brachials rectilinear to slightly cuneate, interlocking laterally. Arms 5. Stem round, heteromorphic.

DESCRIPTION. Crown slender, elongate, 57.3mm long (incomplete), 21.2mm wide, widest at first brachial, tapering distally. Cup medium bowl, 6mm long, 18mm wide, with coarse nodose to irregular ridge ornament, continuing onto brachials; sutures impressed. Infrabasal circlet small, not exposed, may be in shallow impression. Basals 5, convex longitudinally and transversely, proximally forming base of cup, distal part forming base of cup walls, widely outflaring. Radials 5, large, wider (9.5mm) than long (6mm), strongly convex longitudinally, moderately convex transversely, tumid, outflared. Radial facet plenary. Brachials much wider than long (first brachial 4.5mm long, 10.5mm wide), rectilinear to slightly cuneate, moderately convex transversely, straight longitudinally, prominant central longitudinal ridge or keel, with coarse nodose ornament, interlocking laterally, transverse ridges and grooves on lateral ends exterior to pinnular facets; 2 small pinnules on each side, transverse outline angular. Arms 5, tapering distally. Anals not exposed. Stem round, 5mm diameter, heteromorphic; noditaxis pattern N212, cirriferous on second nodal below cup; 53.6mm preserved. Columnals moderately long, (nodals 3.5mm long, internodals 2.6mm long 31mm below cup); latus convex, with coarse nodose ornament proximal to cup, smooth distally. Cirri round, 2.5mm diameter.

REMARKS. The external mould of the crown and proximal stem of the holotype has the distal part of the arms partly disarticulated and central parts of the arms missing. Parts of 4 rays are preserved. The paratype is a set of arms, lacking the cup. The medial ridge on the brachials is well developed on both the holotype and paratype. Measurements taken from latex cast of holotype.

Comparisons are made with species of *Spaniocrinus* and *Parspaniocrinus* because the two genera are closely related. The medium bowl-shaped cup of *S. geniculatus* is lower than that of either *S. validus* Wanner, 1924, *S. transcaucasicus* Yakovlev, 1933 or *Parspaniocrinus beinerti* Strimple, 1971, all of which have truncated medium cones, and *S. trinodus* Weller, 1909 has a much narrower turbinate cup. The coarse nodose ornament of *S. validus* and *S. transcaucasicus*, the triple nodes on the radials of *S. trinodus*, and the fine granular ornament of *P. beinerti*, lack the irregular longitudinal ridges of *S. geniculatus*. Brachials of *P. beinerti* have a rounded exterior in transverse section, whereas brachials of *S. geniculatus* are like the angular transverse outline of *S. validus*. The cup and shorter brachials of *S. geniculatus* are advanced features, probably derived from *S. validus*.

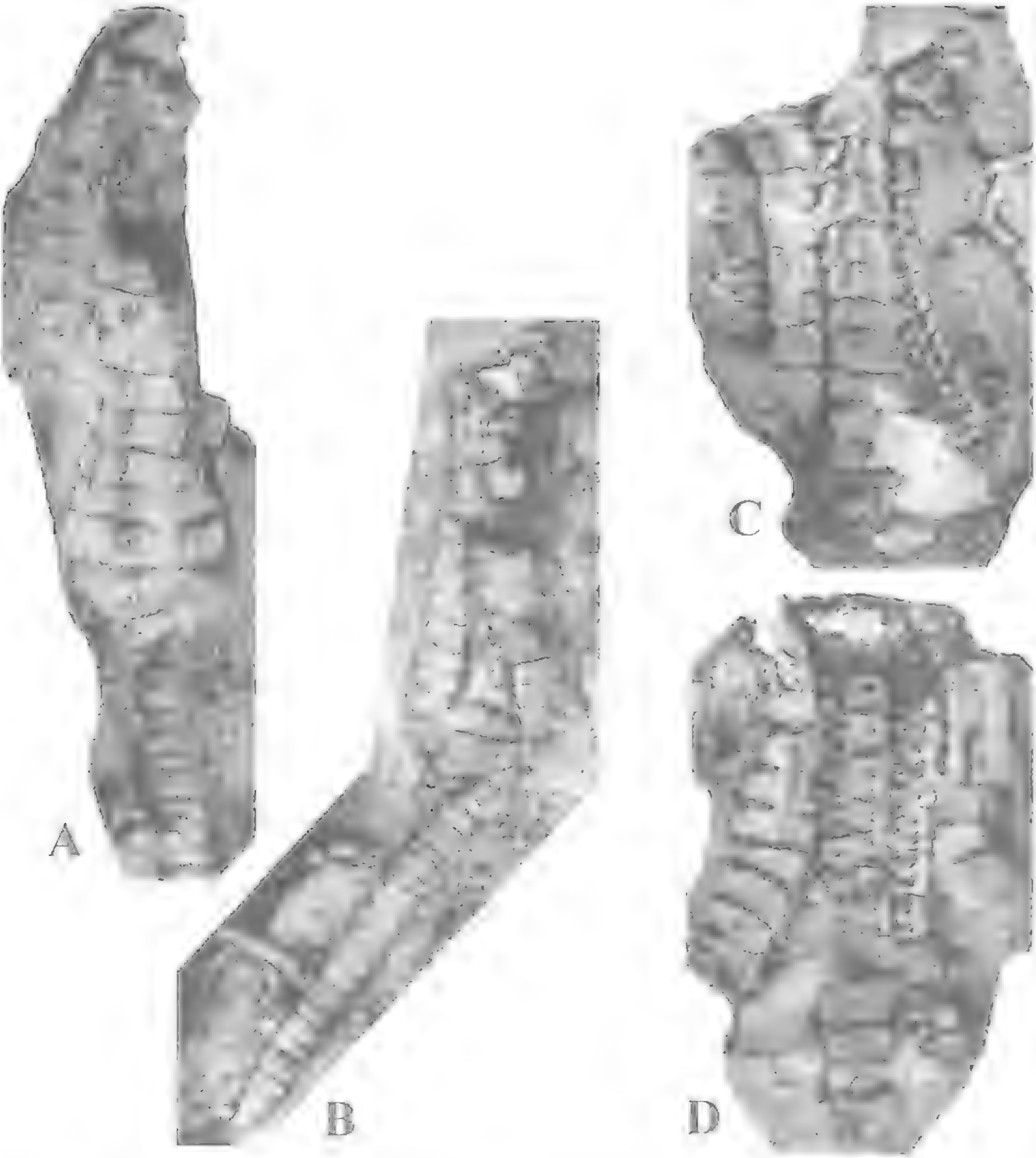


Fig. 9. *Spaniocrinus geniculatus* sp. nov. A,B, enlarged (×1.7) view of ray to left in figure B and lateral view of crown (×1.1), holotype QMF38987. C,D, exterior and interior views of partial set of arms, paratype QMF39011. 1.8.

Superfamily DECADOCRINOIDEA
Bather, 1890
Family DECADOCRINIDAE Bather, 1890

DIAGNOSIS. Moore & Strimple (in Moore & Teichert, 1978: 685) gave the diagnosis as: 'Crown slender. Cup widely expanded, truncate cone or bowl shaped with small basal concavity; five infrabasals with only distal tips at most visible in side view; five medium-sized basals; five radials with articular facets as wide as plates, one to three anals in cup; anal sac tall, slender. Arms ten, formed of cuneate uniserial brachials.

branching isotomously on primibrachs 2 in geologically older forms, and on primibrachs 1 in later ones, no further branching, arms sinuous or zigzag in appearance, pinnules stout, tending to resemble ramules. Stem preponderantly round transversely and noncirriferous (except *Aulocrinus*).'

REMARKS. The Decadocrinidae were recognised primarily on the zigzag nature of the 10 arms and Moore & Strimple (in Moore & Teichert, 1978) considered them intermediate in evolutionary development between some of the genera with rectilinear uniserial arms and some with biserial arms. Taxa with more than 10 zigzag arms were assigned to one of several families based on arm branching patterns and other cup features (i.e. *Plummericrinus* in the Pachylocrinidae; *Spheniscocrinus* in the Ampelocrinidae). Using the zigzag nature of the 10 arms, *Holcocrinus* should have been assigned to the Decadocrinidae instead of the Graphiocrinidae. Without the zigzag appearance of the arms, genera assigned to the Decadocrinidae could have been assigned to the Scytalocrinidae or Graphiocrinidae on the basis of cup shape and number of anals within the cup. However, except for *Parascytalocrinus* all scytalocrinids have a truncated cone-shaped cup. *Parascytalocrinus* was established by Kammer & Ausich (1993) for species with a low bowl-shaped cup with a flat or shallow basal invagination and an atomous A ray previously assigned to *Scytalocrinus*. In the same paper, they erected *Lanecrinus* for species with 10 zigzag arms previously assigned to *Scytalocrinus*. This restricted *Scytalocrinus* to species with conical cups and non zigzag arms.

If the zigzag pattern of the brachials is looked at closely, most genera show that it is dominantly the result of a slight to moderate extension on the long side of the cuneate brachial into a distal shoulder where the pinnule attaches. A node or blunt spine, which accentuates the zigzag appearance when present, may be positioned on the distal shoulder adjacent to the pinnule facet on the outer side of the brachial. *Trautscholdicrinus* lacks the zigzag appearance of the arms, but shows a faint zigzag pattern on the medial keel of the cuneate brachials.

There is considerable difference in the length of the brachials in the Decadocrinidae. The brachials of *Trautscholdicrinus*, *Zostocrinus* and *Eireocrinus* are the longest, *Glaukosocrinus* has intermediate length brachials and all other genera have very short brachials. With the exception of

FIG. 10. *Glaukosocrinus middalyaensis* sp. nov., posterior view of holotype QMF38881, ×2.2.

*Decadocrinus* and *Zostocrinus* they branch on the single primibrachials.

The genera of the Decadocrinidae do not fit into an evolutionary lineage and the family is herein considered polyphyletic. They probably represent advanced taxa evolved from several conservative genera within the cuneate brachial clade recognised by Webster (1997) or other rectilinear brachial genera. Revision of the Decadocrinidae is beyond the scope of this study and should be incorporated in a revision of the Poteriocrinina. Until such a study is completed the Decadocrinidae is retained for convenience.

**Glaukosocrinus** Strimple, 1951

TYPE SPECIES. *Malaiocrinus parviusculus* Moore & Plummer, 1940 from the Desmoinesian Millsap Lake Formation, Parker County, Texas; by original designation.

**Glaukosocrinus middalyaensis** sp. nov.
(Fig.10)

ETMOLOGY. From Middalya Station, WA.

MATERIAL. QMF38881 from QML1240.

DIAGNOSIS. Crown cylindrical, with very fine nodose to vermiform ornamentation; cup with basal invagination; radial facets peneplenary; 3 anals in cup; radianal and anal X large; single axillary primibrach elongate; brachials cuneate; large pinnules relatively short; 10? arms distinctly zigzag; stem round, with narrow crenularium, with wide areola, with round small lumen.

DESCRIPTION. Crown cylindrical, medium size, incomplete length 43.1mm, crushed width 26.4mm, very fine nodose to vermiform ornamentation extending onto arms. Cup medium bowl, shallow basal invagination, crushed length 10mm, crushed width 20mm maximum, 8.2mm minimum. Infrabasals 5, small, horizontal, in basal invagination, not visible in lateral view. Basals 5, medium size, strongly convex longitudinally, moderately convex transversely, forming walls of basal invagination, basal plane, and base of cup walls. Radials 5, large, length 8.2mm, width 9.1mm, gently convex longitudinally and transversely. Radial facet peneplenary, deep, sloping outward strongly. Anals 3; radianal large, 8mm long, 6mm wide, adjoining C radial, CD and DE basals, anal X, and right tube plate; anal X pentagonal, large, 7.8mm long, 6mm wide, widest near distal end. Right tube plate elongate, 5.6mm long, 4.1mm wide, narrowest on proximal end, proximal 1/3 below radial summit. Single primibrach axillary, constricted medially, length 8.1mm, width 7.7mm, widest on proximal end, strongly convex transversely, concave longitudinally. Brachials cuneate, approximately equidimensional, strongly convex transversely, straight longitudinally, with wide pinnule facet on alternating distal ends giving arms distinct zigzag appearance. Pinnules wide, stout, relatively short. Ambulacral groove deep V-shaped. Arms 10? Stem round; facet with narrow crenularium, wide areola, narrow round lumen.

REMARKS. The crown is crushed and cup plates are dislocated in part. The infrabasal circlet was partly exposed by cleaning and barely extends beyond the stem facet. Only 3 basals are preserved and all are distorted by compaction. Solution weathering has destroyed most surface ornament except along part of the D radial, anal X and first tube plate.

*Glaukosocrinus middalyaensis* is distinguished from *G. parviusculus* (Moore & Plummer, 1940) and *G. planus* Strimple & Moore, 1971 by the very fine anastomosing ornament. In addition, the primibrach is longer than that of *G. planus*.

This is the first report of *Glaukosocrinus* outside North America and the first in the Permian. The peneplenary radial facets make relatively narrow radial notches as on the cup of *G. parviusculus*. The arm branching on the single primibrach and shallow basal invagination are advanced features, while the 3 anals in the cup is a primitive feature. These features did not change significantly in the Late Carboniferous or Early Permian.

**Eidosocrinus** gen. nov.

TYPE SPECIES. *Eidosocrinus condaminensis* sp. nov. from the Condamine Beds, Elbow Valley area, near Warwick, SE Queensland.

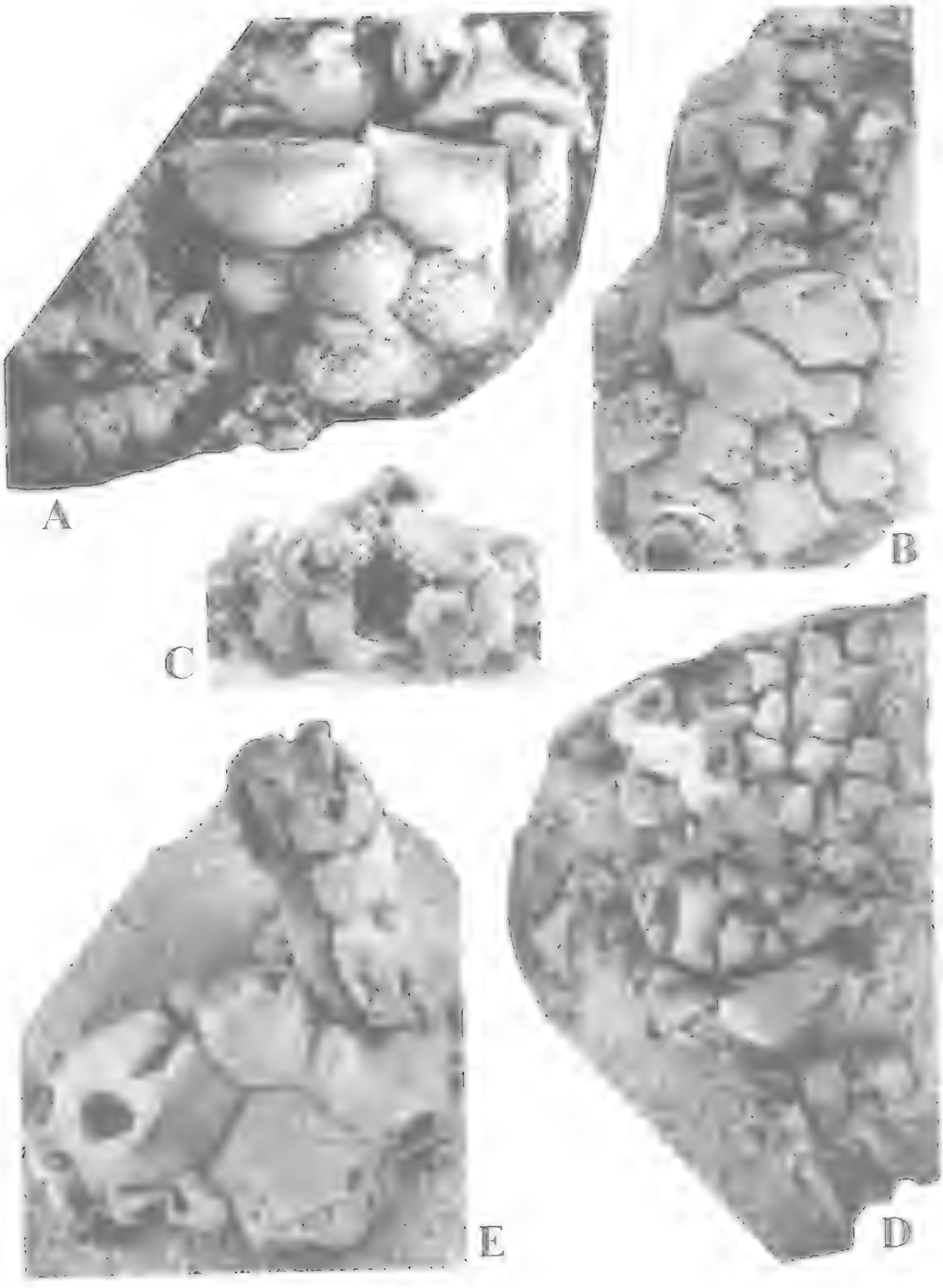
ETYMOLOGY. Greek *eidos*, form or likeness, and *krinon*, lily; refers to the types based on latex casts.

DIAGNOSIS. Crown cylindrical; cup low bowl-shaped, base invaginated, one anal, with single axillary primibrachs of differing lengths in different arms, cuneate brachials, 10 arms zigzag, coarse horn like nodes or blunt spines on the basals, radials, and distal tips of all brachials, fine granulate ornament on basals and radials.

REMARKS. Mild to moderate tumidity of cup and arm plates in the Poteriocrinina is known in *Spheniscocrinus* and *Cromyocrinus*, among others. Likewise, coarse nodes or blunt spines on the axillary brachials are developed on the Pirasocrinidae (*Pirasocrinus*, *Sciadocrinus*) and Zeacrinitidae (*Tholocrinus*), among others. *Triceracrinus* (assigned to the Pirasocrinidae) has coarse horn-like nodes on the basals, radials and primibrachs (similar to those of *Eidosocrinus*), but lacks the nodes on the very short, weakly cuneate secundibrachs that have a medial transverse ridge. Thus, the ornamentation of *Eidosocrinus* is a distinguishing character.

The differing length from ray to ray of the

FIG. 11. *Eidosocrinus condaminensis* sp. nov. A, lateral view of disarticulated partial crown, paratype QMF38904, ×2.6. B, basal view of slightly disarticulated crown, paratype QMF38903, ×2.7. C,D, basal (×2.2) and B ray (x1.8) views of holotype QMF38902. E, internal view of posterior interray, paratype QMF38905, ×4.3.


A
B
C
D
E

axillary primibrachs of *Eidosocrinus* is found in several Scytalocrinidae, Aphelecrinidae, Graphiocrinidae, among other poteriocrininids. This feature is considered intermediate between branching above the first primibrach and on the single primibrach. Combined with features of the cup it may reflect a closer evolutionary relationship of the Scytalocrinidae, Aphelecrinidae and Decadocrinidae than with the rectilinear brachials of the Stachyocrinidae.

**Eidosocrinus condaminensis** sp. nov.
(Fig. 11)

ETYMOLOGY. From the Condamine Beds.

MATERIAL. HOLOTYPE: QMF38902 from QML518 PARATYPES: QMF38903-38905, same.

DIAGNOSIS. As for genus.

DESCRIPTION. Crown incomplete, 34.1mm preserved, cylindrical, ornament of single coarse horn-like node or blunt spine on all basal, radial, and brachial plates. Cup low bowl-shaped, 17.8mm wide, 8.8mm long, base invaginated, fine granular ornament. Infrabasal circlet small, 5.1mm diameter, subhorizontal, not visible in lateral view. Basals 5, 4.5mm long, 5.3mm wide, strongly tumid, outflared, forming base of cup and walls. Radials large, 5mm long, 7.5mm wide, strongly tumid, slightly flaring, forming most of cup wall. Radial facet plenary, subhorizontal, slightly concave transversely, deep, with elevated transverse ridge on central 1/3, deep elongate ligament pit, wide outer margin. Primanal large, 4mm long, 4.7mm wide, very tumid, abutting distally terminated posterior basal, proximal 1/2 in line of radials, distal 1/2 projecting above radial summit, distally adjoined by 2 anal tube plates. Single primibrachs axillary in all rays, A ray longest (8.5mm), C ray intermediate (greater than 4.7mm), B and E rays shortest (4.9mm), strongly convex transversely, concavo-convex longitudinally, hourglass-shape in exterior view. Secundibrachs cuneate, approximately as wide as long, deep, strongly convex transversely, straight proximally becoming convex distally, node adjacent to pinnule facet on long side. Branching isotomously, 10 arms. Stem round, heteromorphic; noditaxis pattern N1. Columnals moderately long; crenularium narrow; lumen small, circular?; latus roundly convex on nodals, gently convex on internodals.

REMARKS. Description of *Eidosocrinus condaminensis* is based on the casts of all types because no specimen is complete. Measurements made on

FIG. 12. A,B, *Eoindocrinus praecontignatus* Arendt, 1981, oblique lateral and lateral views of cup QMF38910, ×5.2. C, *Pedinocrinus? nodosus* sp. nov., C-D interray view of holotype QMF38906, with *E. praecontignatus* cup on arms in upper right, ×1.7.

the holotype. The holotype has part of the D, A, B, and C rays; some cup and arm plates are dislocated slightly. The infrabasal circlet, D-E basal plate, E ray, and anal are lost through weathering. A poorly preserved pluricolumnal in alignment with, directly below, and 6mm from the cup is probably part of the stem. It is round, 2.2mm diameter, heteromorphic (noditaxis

pattern N1) with moderately elongate columnals. Paratype QMF38903 is crushed, all cup plates are slightly dislocated, the proximal columnal nearly covers the infrabasal circlet, and only the proximal part of the E and A rays are preserved. Paratype QMF38904 is also crushed and retains part of the cup, proximal columnals, and primibrach of one ray. Paratype QMF38905 is an internal and external mould of a cup showing the basals, radials, anal, and C ray primibrach. The fine granular ornament is preserved on some cup plates of all 4 specimens.

Tentative assignment of *Eidosocrinus condaminensis* to the Decadocrinidae is for convenience and based primarily on the zigzag nature of the arms.

Superfamily LOPHOCRINOIDEA Bather, 1899
Family STELLAROCRINIDAE Strimple, 1961

**Pedinocrinus** Wright, 1951

TYPE SPECIES. *Pachylocrinus clavatus* Wright, 1937 from the Early Carboniferous, Tournaisian, Lower Limestone Group, Scotland; by original designation.

**Pedinocrinus**? **nodosus** sp. nov.
(Fig. 12C)

ETYMOLOGY. Latin *nodus*, nodes; refers to the nodose ornament of the cup and proximal brachials.

MATERIAL. HOLOTYPE: QMF38906, from QML518.

DIAGNOSIS. Crown flaring distally, cup low bowl-shaped, 3 anals, coarse nodose ornament continuing onto proximal brachials, 1st primibrach, 8th secundibrach and 9th tertibrach axillary; bulbous tegmen; stem round, heteromorphic.

DESCRIPTION. Crown moderately large, 47.7mm long (incomplete), 42.3mm wide (still expanding), pear-shaped, arms flaring. Cup low bowl, 20mm wide (incomplete?), 6.5mm long (estimate), base invaginated. Coarse nodose ornament on all cup plates, primibrachs and proximal 3-4 secundibrachs; all axillary brachials above primibrachs nodose or bearing short blunt spines. Infrabasal circlet not exposed, within impressed basal cavity. Basals relatively small, 4mm long, 4.8mm wide, tumid, moderately convex longitudinally and transversely, subhorizontal to gently upflared. Radials largest cup plates, 3.6mm long, 8.8mm wide, moderately convex transversely, strongly convex longitudinally. Radial facets plenary. Anals 3, moderately large; radianal in CD interray, supporting both rectangular anal X and right tube plate directly above in radial circlet. Brachials cuneate, uniserial to biserial, strongly convex longitudinally and transversely, sutures impressed, one pinnule on widest side. In C ray 1st primibrach, 8th secundibrachs, and 9th tertibrachs axillary, probably 1 or 2 additional branchings distally. All branching isotomous, minimum of 40 arms if all rays branch as in C ray. Arms flare moderately laterally. Anal tube large, probably bulbous, formed of many small polygonal plates. Stem round, heteromorphic; noditaxis of N212 or N1 in proximal 20mm preserved. Columnals with strongly convex latus.

REMARKS. The external mould of *Pedinocrinus*? *nodosus* preserves part of the posterior side of the cup, the proximal parts of the C and D rays including some quartibrachs and tegmen plates. Cup plates are partly dislocated with the C radial nearly covering the right tube plate. The cup is covered by a cladoporid coral in part. All measurements are approximate, from latex casts.

At first glance *P.*? *nodosus* appears to resemble *Plaxocrinus*, *Tholocrinus* and *Hydreionocrinus*, all of which have moderately large flaring crowns with a low bowl-shaped or discoidal cup, axillary brachials bearing short spines or blunt nodes and large inflated tegmens. However, these taxa are placed in different familes based on the number of anals in the cup, type of brachials, and arm branching patterns. These taxa range in age from Early Carboniferous into the Late Permian and represent heteromorphic evolution within different lineages of the poteriocrininids in the late Palaeozoic.

Lacking ornamentation this specimen would be placed in *Pedinocrinus* without question. Arguments could be made for erecting a new genus for *P.*? *nodosus*. However, we do not believe that ornament alone is sufficient for establishing a new genus. The significant time gap between the Tournaisian *P. clavatus* (Wright, 1937) and the Artinskian *P.*? *nodosus* suggests *Pedinocrinus* may be a holdover in Australia. The coarse nodose ornament on the cup plates and proximal brachials of *P.*? *nodosus* should assist future recognition.

**Stellarocrinid**? gen. et sp. nov.
(Fig. 13C)

MATERIAL. UQF12211A, from QML518.

DESCRIPTION. Cup unknown. Arms broad, widespread. Brachials uniserial, 4.6mm long, 11.5mm wide, mildly cuneate, deep, with coarse

nodose ornament; with very large blunt node elongated parallel to arm length on inner side of long end, with notch for pinnule facet on outer side of short end. Ambulacral groove large, 2mm wide, V-shaped, joined by side grooves from short end of brachials. C and D ray arms branching isotomously on single primibrach, may branch again distally. Branches widely flared laterally. Tegmen formed of several inflated small (3.6mm diameter) to medium sized (7mm diameter) polygonal plates adjacent to 2 inflated very large orals (11mm diameter) at base of large anal tube (19mm diameter). Base of anal tube formed of 5 columns of vertically stacked plicate hexagonal plates (5.6mm long, 6.4mm wide); anal tube length unknown. Additional columns of tegmen plates not preserved, estimated minimum of 4 or 5 present. Smaller (3.6mm long and wide) anal tube plates projecting outward from the 3rd row of tube plates.

REMARKS. The specimen is an external mould of the oral surface of a large partial crown consisting of parts of 7 arms probably belonging to 5 rays. The 2 arms of the C and D rays branch close to the tegmen and the ambulacral groove of each of the 2 adjacent arms (B and E rays) join the ambulacral groove of the C and D rays before passing into the interior of the tegmen. It could be proposed that each of these sets of 3 arms are part of 1 ray, which would require 2 more rays behind the tegmen and not preserved. This is not likely with the excellent preservation and spacing of the arms. The 7th arm, the A ray, is undivided on the preserved part. The distal end of the E ray is regenerated, as distal brachials are much smaller than proximal brachials. The first brachial of the regenerated section is axillary. All arms probably branch again distally. All measurements are approximate, taken from a latex cast.

Although pinnules are not preserved their presence is presumed because notches for their attachment are present on the outer side of the brachials and a large U-shaped ambulacral groove along the short end of the brachial adjoins the main ambulacral groove. Attachment of the pinnules to the short end of the brachials is an exception to the normal attachment on the long end. Both the development of the large nodes on the inside of the long end of the brachial and the pinnule attachment on the short end are considered evolutionary developments of the specimen, not known in other poteriocrininids.

The small anal tube plates projecting laterally from the anal tube probably represent the distal parts of a recurved anal tube. The plates are slightly disarticulated and adjoined more distal plates that are not preserved.

The specimen represents a new genus but is considered inadequate to serve as a holotype, lacking the cup. It is assigned to the stellarocrinids because the laterally projecting arms spread widely, structure of the large elongate anal tube, presumed branching pattern of the arms, and cuneate brachials bear coarse ornamentation. These are all features of the stellarocrinids.

### Family SUNDACRINIDAE Moore & Laudon, 1943

### **Sundacrinus** Wanner, 1916

TYPE SPECIES. *Sundacrinus granulatus* Wanner, 1916 from the Permian Basleo Beds, Timor; by original designation.

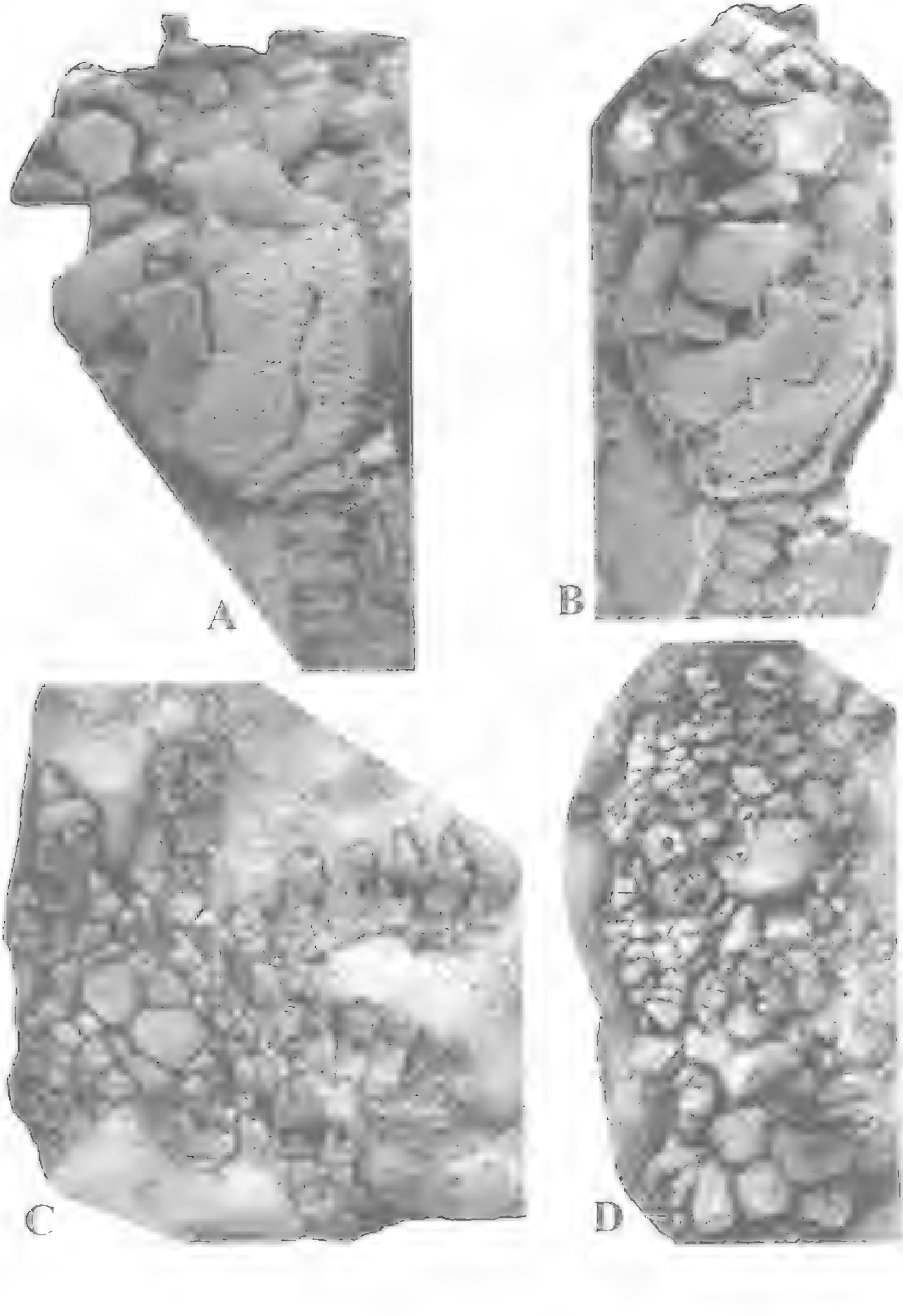
### **Sundacrinus medius** sp. nov. (Fig. 13A,B)

ETYMOLOGY. Latin *medius*, middle; refers to the cup shape intermediate between that of 2 previously described species.

MATERIAL. QMF38908 from QML518.

DESCRIPTION. Crown medium size, pear-shaped, 32.4mm long (incomplete), 19.6mm wide. Cup medium to high bowl-shaped, 13mm long, 18.6mm wide at radial summit, base gently upflared, all plates very thick with coarse nodose ornament grading into irregular anastamosing ridges. Infrabasal circlet large, 9.5mm diameter, gently upflared, visible in lateral view. Basals largest plates in cup, gently convex longitudinally and transversely, widely flaring, of variable size and shape; posterior basal hexagonal, 7.5mm long, 8.4mm wide, adjoining radianal, BC basal, infrabasals, CD basal, D radial and anal X. Radials large, 6.5mm long, 7.5mm wide, subvertical to slightly incurved distally, weakly convex longitudinally and transversely. Radial facet plenary, strong outward-downward slope. Two pentagonal anals in cup; radianal largest, adjoining C radial, BC and CD Basals, anal X, and first tube plate, distal tip projecting slightly above radial summit; anal X adjoining radianal, CD basal, D

FIG. 13. A,B, *Sundacrinus medius* sp. nov., posterior and D ray views of holotype, QMF38908, ×2.6. C, Stellarocrinid? gen. et sp. nov., oral view of tegmen and arms, UQF12211A, ×1. D, *Moapacrinus cuneatus* sp. nov., posterior view of slightly disarticulated crown, holotype, QMF38909, ×1.9.


A
B
C
D

radial, D primibrach, and overlying tube plate, distal 1/3 above radial summit. D ray primibrach elongate, straight longitudinally, strongly convex transversely, may be axillary. Secundibrachs cuneate uniserial, elongate, deep, straight longitudinally, strongly convex transversely, with wide V-shaped ambulacral groove. Anal tube stout, projecting above cup, formed of thick hexagonal plates of uncertain structural pattern, probably laterally interlocked stacked columns, length unknown. Stem round transversely, 4.5mm diameter, heteromorphic, of variable noditaxis pattern in 24mm length preserved, at least 4 distinct sizes of columnals; latus moderately to strongly convex.

REMARKS. This partial crown consists of a slightly crushed cup below a jumbled pile of dislocated brachials and anal tube plates. It is assigned to *Sundacrinus* based on cup shape, thick plates, plenary radial facet sloping outward-downward and irregular shape of cup plates.

*Sundacrinus medius* has a cup shape intermediate between the conical cup of *S. triangulus* Wanner, 1924 and the bowl-shaped cups of *S. granulatus* Wanner, 1916 and *S. vastus* Wanner, 1924. The elongate cup of *S. elongatus* is much more slender than that of *S. medius*. Moore et al. (in Moore & Teichert, 1978) recognised that the number of anals in *Sundacrinus* varied, reporting 1, rarely 2. However, there are 2 in *S.* cf. *vastus* (Wanner, 1937, pl. 10, fig. 25) and 3 in *S. triangulus* (Wanner, 1937, pl. 10, fig. 21). Thus 2 anals in *S. medius* is intermediate.

This is the first report of the anal tube of *Sundacrinus* and the first report of the genus in Australia. It provides additional support for interconnections of E Australia and Timor.

Superfamily CROMYOCRINOIDEA Bather, 1890
Family CROMYOCRINIDAE Bather, 1890

**Moapacrinus** Lane & Webster, 1966

TYPE SPECIES. *Moapacrinus rotundatus* Lane & Webster, 1966 from the Artinskian part of the Bird Spring Formation, Nevada; by original designation.

**Moapacrinus cuneatus** sp. nov.
(Fig. 13D)

ETYMOLOGY. Latin *cuneatus*, wedge-shaped.

MATERIAL. HOLOTYPE: a crushed, partly disarticulated, partial crown, QMF38909 from QML518.

DIAGNOSIS. Crown elongate, cup medium bowl-shaped, shallow basal invagination, sutures impressed, coarse nodose ornament, single large anal, axillary 1st primibrach, brachials strongly cuneate.

DESCRIPTION. Crown elongate, 46.2mm long, incomplete. Cup medium bowl-shaped, 7.6mm long, 16mm wide, shallow basal invagination, sutures impressed, coarse nodose ornament, slightly incurved at radial summit. Infrabasal circlet not visible in lateral view. Basals large, 5.3mm long, 6.7mm wide, strongly convex longitudinally and transversely, forming base of cup and lower part of cup wall. Radials of intermediate size, 4.8mm long, 8.1mm wide, moderately convex longitudinally and transversely, subvertical. Radial facet plenary, deep; transverse ridge slightly concave externally; ligament pit elongate, deep; narrow outer margin; muscle fields large, intermuscular furrow shallow.

Single anal large, 4.5mm long, 5.2mm wide, directly above posterior basal, distal 2/3 above radial summit. Single primibrach axillary. Brachials uniserial, strongly cuneate, gently convex longitudinally, strongly convex transversely; 10 arms.

REMARKS. *Moapacrinus cuneatus* has wedge-shaped brachials and is ornamented with coarse nodes, whereas other species of the genus have rectilinear brachials and lack coarse nodose ornament. Pabian & Strimple (1993) reported fine granular ornament on *M. elexensis* Pabian & Strimple, 1993 known only from a cup. Only the posterior 1/2 of the cup of *M. cuneatus* is exposed; the C and D ray arms are dislocated and brachials partly disarticulated.

This is the first report of *Moapacrinus* outside North America, the first record of a cromyocrinid in E Australia, and the youngest cromyocrinid known. Cromyocrinids are common in late Palaeozoic faunas of the Midcontinent and Rocky Mountain regions of the USA. Pabian et al. (1989) reported the cromyocrinids in their 'Terrigenous Facies Belt', implying some clastic sediment entering the living environment. Webster & Houck (1998) noted that cromyocrinids dominate Late Carboniferous faunas in intermontane basin settings of the Rocky Mountain region. Although carbonates dominated the environment, some sand size clastic sediment was deposited wherein the cromyocrinids were living. Thus, a cromyocrinid was probably well adapted for living in the mudstone environment of the Condamine Beds.

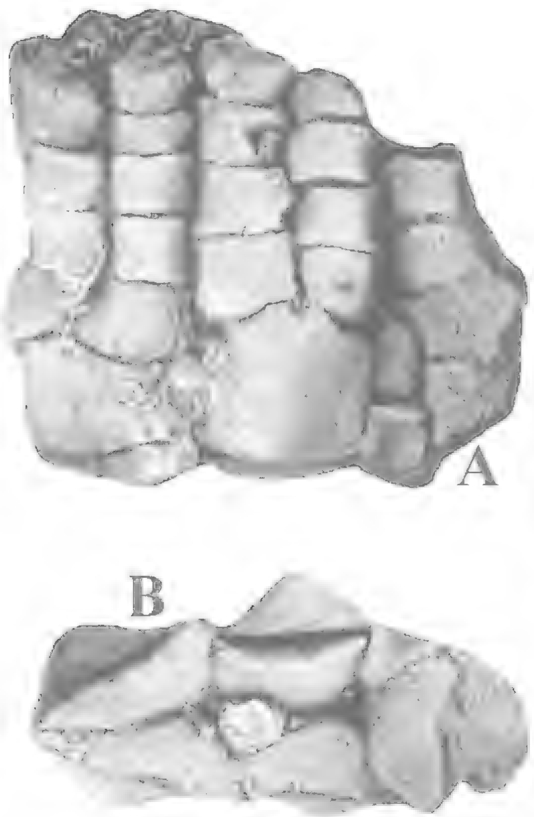



FIG. 14. A, B, *Parabursacrinus granulatus* Wanner, 1949, D ray and basal views of crushed crown QMF38882, ×3.2.

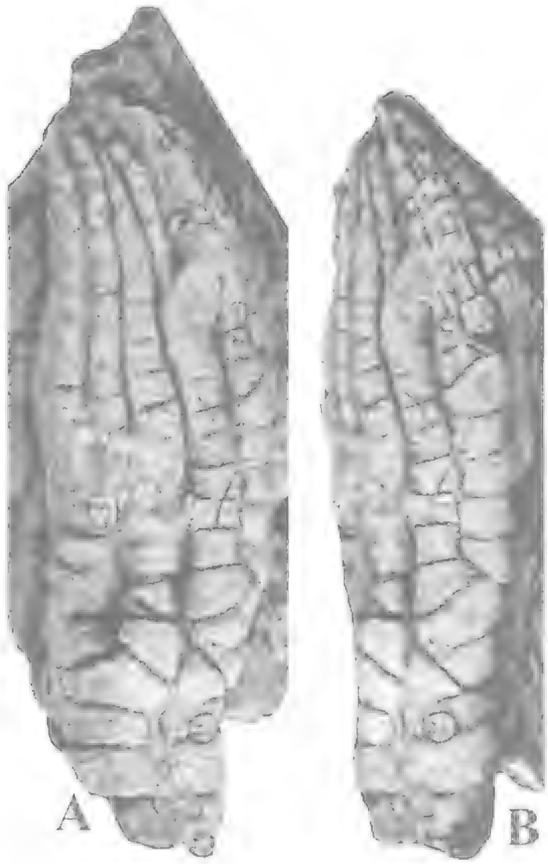



FIG. 15. A,B, Timorechinid gen. indet., lateral views of partial set of arms QMF38883, ×3.3.

### Family INDOCRINIDAE Strimple, 1966

#### **Eoindocrinus** Arendt, 1981

TYPE SPECIES. *Eoindocrinus praerimosus* Arendt, 1981 from the late Artinskian Sarginsk Horizon, Ural Mts; by original designation.

#### **Eoindocrinus praecontignatus** Arendt, 1981 (Fig. 12A,B)

MATERIAL. External mould of cup, QMF38910 from QML518.

REMARKS. This small cup (5.4mm long, 5.8mm wide), on the arms of *Pedinocrinus*? *nodosus*, is oriented on its side with the C-D basal centred, the basal circlet upturned and the oral rim crushed downward (not visible). The large stellate ridge ornament converges in the centre of the basals and forms triangles across adjacent plates. Smaller inflated triangles are formed within these at the apices of triple plate junctions. A ridge junction also occurs on the radianal which supports the right tube plate distally and is adjacent to anal X.

A specimen of *E. praecontignatus* from the Wandagee Sandstone of Western Australia has partly developed secondary ridges forming a secondary triangle within the primary ridge triangle (Webster, 1990). The Condamine and Wandagee forms are considered conspecific with variation in ornament comparable to that in *E. praecontignatus* from the Urals (Arendt,1981).

### Superfamily ZEACRINITOIDEA Bassler & Moodey, 1943
### Family ZEACRINITIDAE Bassler & Moodey, 1943

#### **Parabursacrinus** Wanner, 1924

TYPE SPECIES. *Bursacrinus procerus* Wanner, 1916 from the Basleo Beds, Timor, by original designation.

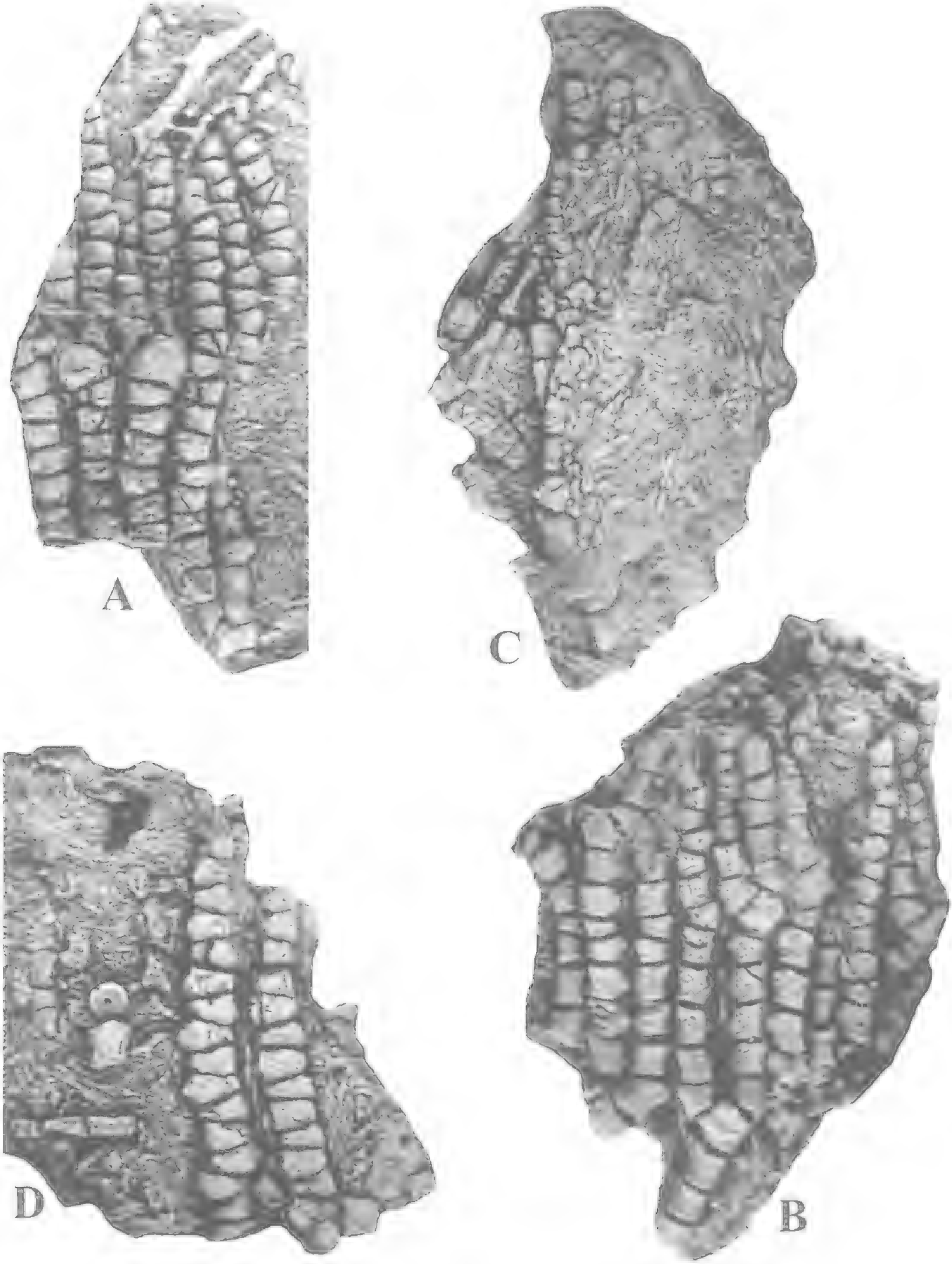



FIG. 16. A,B, Poteriocrinitid indet., arms 1. A, lateral view of QMF38885, ×3.2. B, lateral view of QMF38884, ×3.1. C,D, Poteriocrinitid indet., arms 3, interior (×3) and exterior (×4) lateral views of QMF38887, ×4.

**Parabursacrinus granulatus** Wanner, 1949
(Fig. 14)

MATERIAL. QMF38882 from QML1232.

REMARKS. This small crown is probably an immature or young adult. It is crushed against the C-EA axis, infrabasals and basals are not visible and distal parts of the arms are lost. The single anal projects 1/2 above the radial summit. Arms all bifurcate on the 1st primibrach. Granulose ornament continues onto the rectilinear brachials. Heteromorphic proximal stem columnals are round in section.

Family TIMORECHINIDAE Jaekel, 1918

**Timorechinid** gen. indet.
(Fig. 15)

MATERIAL. QMF38883 from QML1237.

DESCRIPTION. Arm fragment incomplete, slender, 32mm long, 13.5mm wide, parts of , or possibly 4 rays present. Arms 3, slender. Brachials uniserial, rectilinear, gently convex longitudinally, moderately convex transversely. Isotomous branching on 4th and 5th brachials, again on 4th and 5th brachials on outer 1/2 of arm, probably endotomous. Pinnules and ambulacral groove not visible.

REMARKS. This specimen has the arms enclosed, is crushed, and probably represents parts of 3 rays. The main part visible is judged to represent 1 ray which had bifurcated isotomously below the preserved part. As interpreted there are 6 arms in the ray, total of 30 arms if all rays bifurcate uniformly. Brachials and arm branching pattern of this type occur in *Notiocrinus* and *Parabursacrinus* of the Timorechinidae to which the specimen is referred.

**Poteriocrinitid** indet., arms 1
(Fig. 16A,B)

MATERIAL. QMF38884 and 38885 from QML1237.

DESCRIPTION. Fragment 1. Arms slender, elongate; fragment 29.2mm long, 19.4mm wide, incomplete, including medial portions of a minimum of 16 arms with one additional distal branching on most arms. Brachials rectilinear to moderately cuneate, gently convex longitudinally, strongly convex transversely. Axillary brachials strongly protruded. One slender pinnule per brachial on alternate sides of arm. All branchings isotomous, but only branch on one half of arm distally, probably endotomous.

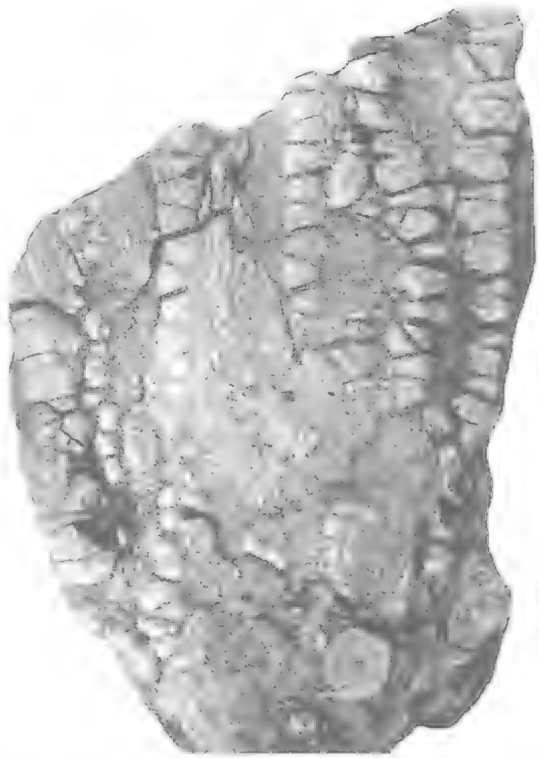


FIG. 17. Poteriocrinitid indet., arms 2, lateral view of QMF38886, ×1.8.

Fragment 2. 32mm long, 14mm wide, incomplete, medial portions of a minimum of 9 arms. Description as for fragment 1.

REMARKS. These 2 fragments may belong to a single specimen as they were found within 15 cm of one another. They are the medial and distal parts of the arms and, if from 1 specimen, there were a minimum of 40 arms. In the enclosed position the arms have a jointed or knotted appearance at the branchings, similar to those of several poteriocrinitids, such as *Abrotocrinus* and *Anchicrinus*.

**Poteriocrinitid** indet., arms 2
(Fig. 17)

MATERIAL. QMF38886 from QML1240.

DESCRIPTION. Partial set of arms 53.8mm long, 39.5mm wide, incomplete, arms unbranched, loosely parallel. Brachials medium size, moderately cuneate, straight to weakly convex longitudinally, roundly convex transversely, with pinnule on long end; ambulacral groove shallow, rounded V shape.

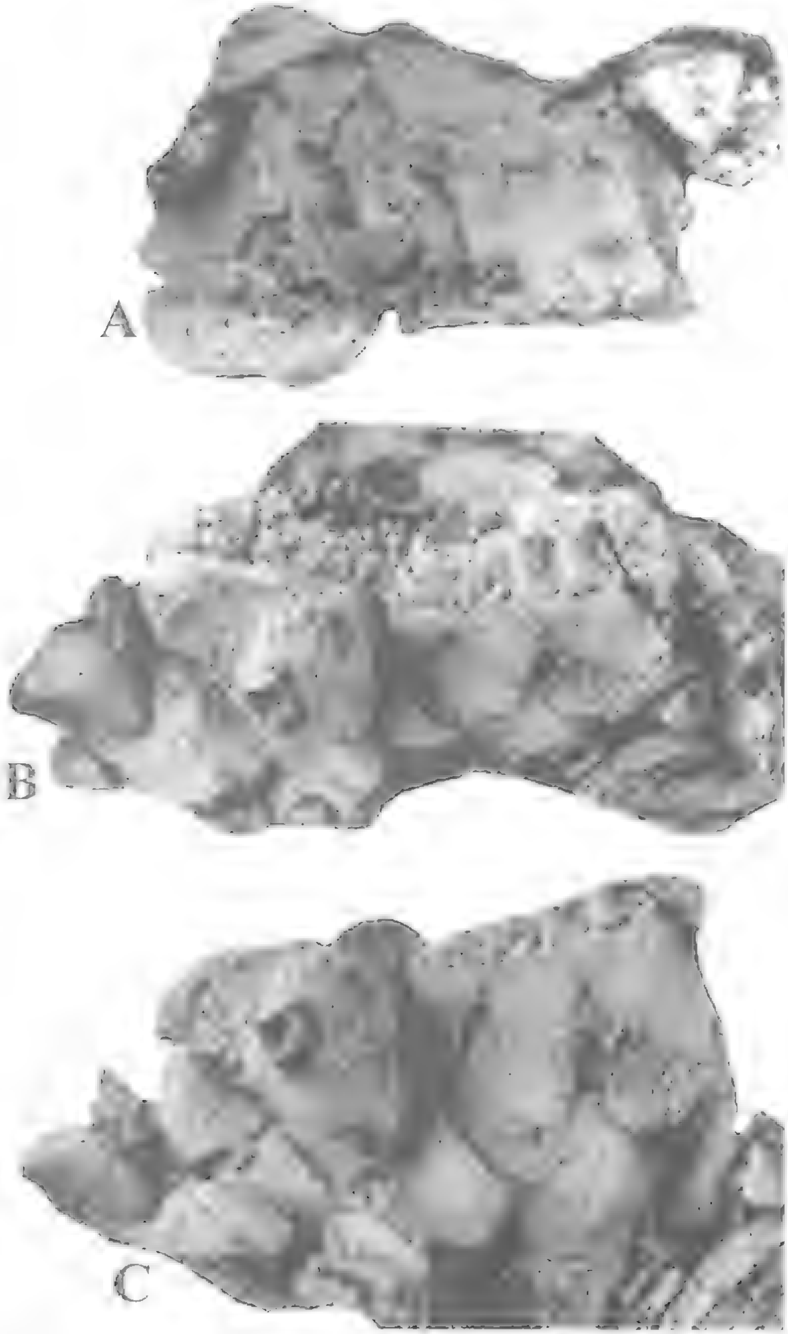



FIG. 18. A-C, Poteriocrinitid indet., arm fragment 1, oral, lateral and exterior views, QMF38911, ×2.5.

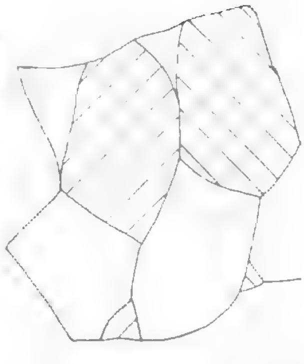


FIG. 19. Poteriocrinitid indet., arm fragment 1, camera lucida sketch of exterior surface of 4 brachials shown in Fig. 18C, ×3. Similar parallel ruled sections are external parts of a single brachial.

REMARKS. The arms have a slight zigzag appearance as a result of weathering, especially the long pinnule bearing end of the brachials with greater relief. Where there is little weathering the zigzag is slight. Nine arms are present on the 2 sides of the specimen. It is not known if the A ray was unbranched and there were only 9 arms or a 10th arm was lost with weathering. These arms are similar to a number of poteriocrinitids, especially some scytalocrinids and decadocrinids.

**Poteriocrinitid** indet., arms 3
(Fig. 16C,D)

MATERIAL. QMF38887 from QML1237.

DESCRIPTION. Arm fragment 30mm long, 17.9mm wide, with parts of 10 unbranched arms. Arms slender. Brachials uniserial, strongly cuneate, gently convex longitudinally, strongly convex transversely. Ambulacral groove wide, open rounded V-shaped. One slender pinnule per brachial on long end.

REMARKS. The specimen represents the distal part of a minimum of 10 arms, which may represent only 1/2 the arms of the specimen as the pinnules and interior of the arms are visible on 1

side of the small slab, the exterior of 4 arms on the other side and some arms between these are visible in end view.

**Poteriocrinitid** indet., arm fragment 1
(Figs 18, 19)

MATERIAL. QMF38911 from QML518.

DESCRIPTION. Fragment, very large 29.2mm long, 25.2mm wide, 10.5mm deep, consisting of 8 brachials. Single brachial 7.8mm long, 25.2mm wide, 10.5mm deep. Brachials uniserial but appearing biserial (=pseudobiserial). In exterior view each brachial divided into 2 parts; larger pentagonal section borders 2 adjacent brachials in middle of arm in apparent biserial interlocking fashion, sides adjoining 2 pentagonal sections of alternate brachials, end forming arm margin with pinnule facet; smaller section triangular, longer isosceles sides tapering toward centre of arm, adjoining adjacent brachials on either side, shorter 3rd side forming arm margin with pinnule facet. Both sections convex longitudinally and transversely, continuous beneath the 2 adjacent brachial sections. Interior convex with central small V-shaped ambulacral groove.

REMARKS. These brachials are the largest known for Palaeozoic crinoids, the only known pseudobiserial form, and one of the few bipinnular forms, bearing one pinnule on each end of a compound brachial. The bipinnular condition of *Zeacrinus* is a minimal form of hyperpinnulation. Hyperpinnulation, in which multiple pinnules are present on both sides of the arms, developed in a few camerates (*Briarocrinus*, 4 per brachial, 2 on each side) and poteriocrinitids (*Cupressocrinites*, 6 or 8 per brachial, 3 or 4 on each side; *Neozeacrinus*, 4 per brachial, 2 on each side). Hyperpinnulation is thought to have developed by fusion of adjacent brachials (Ubaghs in Moore & Teichert, 1978).

Development of the pseudobiserial form requires overlapping of the 2 adjacent brachials, as well as the bipinnular condition. The following possible origins are suggested. First, that they evolved by fusion of 2 cuneate uniserial brachials, one becoming the shorter end and the other the longer end, each bearing a pinnule, with simultaneous overgrowth of the 2 adjacent brachials. Second, that they evolved from biserial brachials in which 2 pinnule bearing brachials fuse at the midline with the simultaneous overgrowth of the 2 adjacent brachials. Third, that they evolved from cuneate brachials with development of a pinnule on the short non pinnule bearing end of a brachial, concurrent with overgrowth of the 2 adjacent brachials. The 1st or 2nd origin is most likely as the 3rd requires redevelopment of a pinnule on a non pinnule bearing end of a brachial.

Although no pinnules are attached to the brachials, 2 ossicles adjacent to the arm fragment are pinnulars, both with the wide V-shaped ambulacral goove exposed. The largest is 5mm long, 5mm wide and 3.5mm deep; the ambulacral groove is 1.5mm wide and 0.6mm deep. Their size and association with the arm fragment suggest that they belong to 1 species.

**Poteriocrinitid** indet., arm fragment 2
(Fig. 20B,C)

MATERIAL. QMF38912 from QML518.

DESCRIPTION. Arm large, 59mm long (incomplete), unbranched. Brachials large, (proximal brachial 4mm long on wide end, 7mm deep, estimated 8mm wide) strongly cuneate, biserial proximally, uniserial distallly, straight to gently convex longitudinally, strongly convex transversely, with large pinnule on wide end, ambulacral groove large, V-shaped. Proximal pinnule 3mm long, 4mm deep, concave longitudinally, strongly convex transversely. More distal pinnules slender, elongate, concave longitudinally, strongly convex transversely.

REMARKS. This arm fragment is curved backwards in a feeding or death posture. Pinnules are larger than brachials of many crinoids. It probably belongs to an unknown poteriocrininid.

**Poteriocrinitid** indet., arm fragment 3
(Fig. 20A)

MATERIAL. QMF39013 from QML518.

DESCRIPTION. Brachials large, 3.3mm long, 4.8mm wide, moderately cuneate, slightly convex longitudinally, strongly rounded transversely, coarse nodose ornament; single pinnule on long end, pinnulars slender, elongate. Anal tube slender, formed of irregularly arranged polygonal plates with coarse nodose ornament; basal plate of tube with sharply pointed centrally expanded spine.

REMARKS. The nodose ornament is randomly distributed externally with up to 20 on a single brachial. Nodose brachials occur in several Condamine fauna species. Nodes are more numerous and smaller on Poteriocrinitid indet., arm fragment 3 than on *Pedinocrinus*? *nodosus* and coarser than on *Poteriocrinites*? *smithii* Etheridge, 1892.

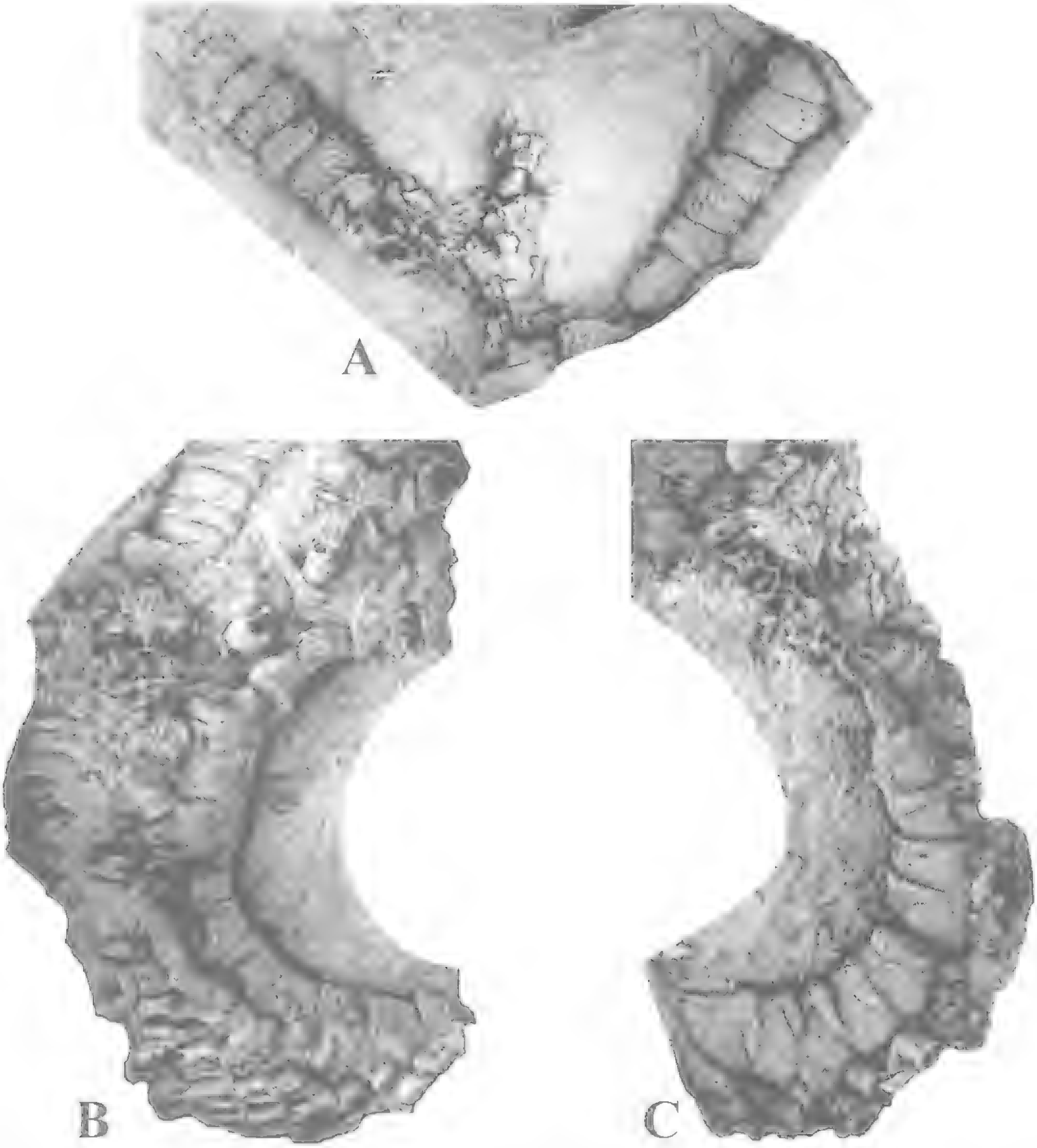


FIG. 20. A, Poteriocrinitid indet., arm fragment 3, lateral view, QMF39013, ×2. B,C, Poteriocrinitid indet., arm fragment 2, counterpart lateral views, QMF38912, ×1.7.

Subclass FLEXIBILIA Zittel, 1895
Order SAGENOCRINIDA Springer, 1913
Superfamily LECANOCRINOIDEA Springer, 1913
Family MESPILOCRINIDAE Jaekel, 1918

**Loxocrinus** Wanner, 1916

TYPE SPECIES. *Loxocrinus globulus* Wanner, 1916 from the Basleo Beds, Timor, by original designation.

**Loxocrinus booni** Marez Oyens, 1940
(Fig. 21E,F)

MATERIAL. QMF38888 from QML759.

REMARKS. This partial cup consists of the D and E radials and distal tip of the DE basal, if the A radial is symmetrical. The cup is low bowl-shaped with the infrabasals probably not visible in lateral view. It is slightly abraded and

encrusted with bryozoans. Radial facets of the short, thick radial plates are shifted to the right of centre with the left shoulder wider than the right. The facets are concave, deep with a narrow rim of crenulae and culmina along the rounded outer edge; other details of the surface are lost by solution or covered by encrusting organisms.

Only *L. booni* has a low bowl-shaped cup with the infrabasals not visible in lateral view, as the other 2 species, *L. globulus* Wanner, 1916 and *L. dilatatus* Wanner, 1916, are globose with the infrabasals visible in lateral view.

**Loxocrinus** sp. 1
(Fig. 22A)

MATERIAL. QMF38889 from QML757.

DESCRIPTION. Radial small, 5mm long, 5.1mm wide, thick, proximally straight longitudinally, distally incurved, moderately convex transversely, fine granular to vermiform ornament; shoulders extended longitudinally, left shoulder wider than right, both wrapping around radial facet to ambulacral groove. Radial facet angustary, skewed right of centre, elliptical in outline, concave with marginal rim; transverse ridge aboral of centre, low; ligament pit in centre of radial, small, transversely elongate; outer marginal area crescent-shaped; muscle areas large, with irregular surface; ambulacral groove moderately wide V shaped, confined to adoral edge of facet.

REMARKS. If the radial facet of *Loxocrinus* sp. 2 were horizontal, the radial sloped inward for its entire length. Most likely the radial facet sloped downward, outward and the proximal part of the radial was vertical with the distal part curving inward. The shoulders left small obvious notches between arm bases. The specimen is the D or E radial if the A radial is symmetrical.

**Loxocrinus** sp. 2
(Fig. 22B,C)

MATERIAL. QMF38890, 38891 from QML758.

DESCRIPTION. Radial small, thick, proximally straight longitudinally, distally incurved, moderately convex transversely, unornamented; shoulders extended longitudinally, left shoulder wider than right, wrapping around radial facet to ambulacral groove, right shoulder terminating against radial facet adoral of transverse ridge. Radial facet angustary, skewed right and left of centre, nearly circular in outline with extended right side muscle area, concave with marginal rim; elevated transverse ridge 3/4 of distance aboral of facet; ligament pit aboral of centre of and culmina on aboral 1/2; muscle areas large, irregular surface; ambulacral groove moderately wide V-shaped, notched into adoral 1/4 of facet. QMF38891 8.1mm long, 7.6mm wide; QMF38890 8.2mm long, 10.1mm wide.

REMARKS. Orientation of *Loxocrinus* sp. 2 would have been very similar to *L.* sp. 1. The two forms are distinguished by the lack of ornamentation on *L.* sp. 2. They both differ from *L. booni* by being much longer. QMF38891 is the D or E radial, if the A radial is symmetrical, as the facet is skewed to the right and the facet shows evidence of solution weathering. QMF38890 is the B or C radial with the facet skewed to the left.

Family PROPHYLLOCRINIDAE Moore & Strimple, 1973

**Prophyllocrinus** Wanner, 1916

TYPE SPECIES. *Prophyllocrinus dentatus* Wanner, 1916 from the Basleo Beds, Timor; by original designation.

**Prophyllocrinus** sp. 1
(Fig. 21A)

MATERIAL. QMF38892 from QML758.

DESCRIPTION. Radial medium size, 10.8mm long (incomplete), 10.4mm wide, medium depth, proximally straight longitudinally, distally incurved, moderately convex transversely, fine granular ornament; shoulders greatly extended longitudinally, left shoulder wider than right, extending slightly beyond radial facet, right shoulder broken off, probably terminating against distal end of radial facet. Radial facet angustary, skewed right of centre, elongate U-shaped, concave with marginal rim; elevated transverse ridge 3/4 aboral length of facet; ligament pit small, centre of radial; outer marginal area crescent-shaped; muscle areas large, shallowly concave; ambulacral groove deep, wide V-shaped, notched into adoral 1/2 of facet.

REMARKS. Solution etching has destroyed the proximal edge of the radial and some surface features of the transverse ridge and ligament pit of the radial facet. The right shoulder and a small piece of the left edge of the outer margin of the radial facet were broken off. The long U-shaped radial facet readily distinguishes the specimen from those of *Loxocrinus* and allies it with *Prophyllocrinus*. Breakage suggests a very short right shoulder, a character of *Proapsiocrinus* and *Ancistrocrinus*.

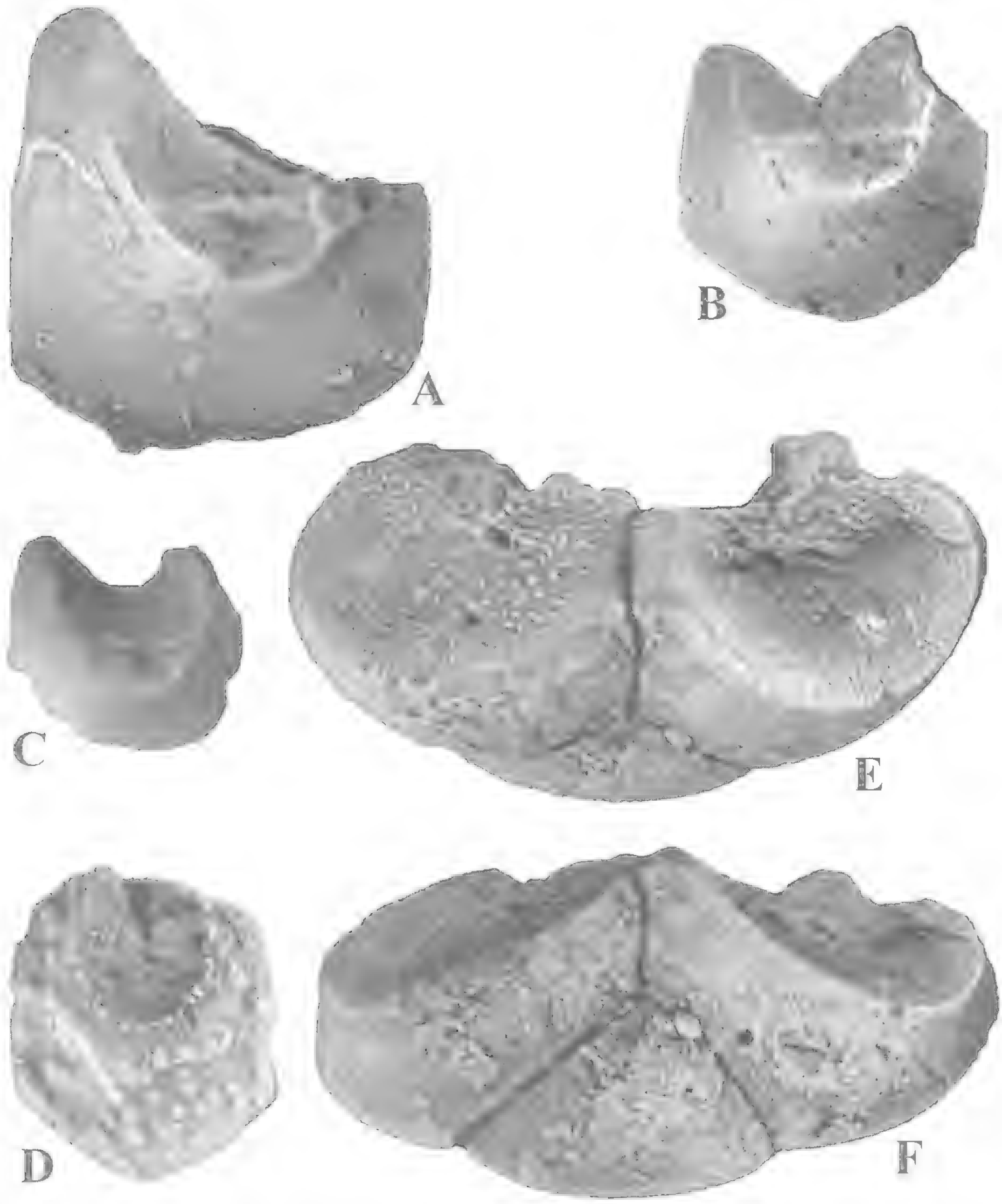


FIG. 21. A, *Prophyllocrinus* sp. 1, lateral view of radial QMF38892, ×5.7. B,C, *Prophyllocrinus* sp. 2. B, lateral vieof radial QMF38893, ×4.4. C, lateral view of radial QMF 38894, ×4.1. D, *Prophyllocrinus* sp. 3, lateral view of radial QMF38895, ×9.2. E,F, *Loxocrinus booni* Marez Oyens, 1940, oral and lateral views, QMF38888, ×5.5.

**Prophyllocrinus** sp. 2
(Fig. 21B,C)

MATERIAL. Radials QMF38893 from QML758 and QMF38894 from QML757.

DESCRIPTION. Radial medium size and thickness, proximally straight longitudinally, distally incurved, moderately convex transversely, no ornament; shoulders greatly extended

longitudinally, left shoulder longer than right, both terminate against distal end of radial facet. Radial facet angustary, skewed right of centre, elongate U-shaped, concave with marginal rim; elevated transverse ridge 3/4 aboral length of facet; ligament pit very small, centre of radial; outer marginal area crescent-shaped; muscle areas large, shallowly concave; ambulacral groove deep, wide V-shaped, notched into adoral 1/2 of facet. QMF38893 10.3mm long (incomplete), QMF38894 8mm long, 7.9mm wide (both incomplete).

REMARKS. QMF38893 lacks the distal end of the right shoulder, the proximal edge of the radial and adoral edge of the ambulacral groove from solution etching. Solution etching has destroyed the proximal edge of the radial, some surface features of the transverse ridge and ligament pit of the radial facet and distal parts of the muscle area and ambulacral groove of QMF38894. *Prophyllocrinus* sp. 2 differs from *P.* sp. 1 by lacking ornament.

**Prophyllocrinus** sp. 3
(Fig. 21D)

MATERIAL. QMF38895 from QML758.

DESCRIPTION. Radial small, 4.9mm long, 4.6mm wide, medium depth, proximally straight longitudinally, distally incurved, moderately convex transversely, with coarse granular ornament; shoulders greatly extended longitudinally, left shoulder longer than right. Radial facet angustary, skewed right of centre, elongate U-shaped, concave with marginal rim; elevated wide transverse ridge located close to ambulacral groove at 1/3 adoral length of facet; ligament pit very small; outer marginal area crescent-shaped; muscle areas small, shallowly concave; ambulacral groove narrow V-shaped, notched into adoral 1/3 of facet.

REMARKS. Solution etching has destroyed the distal end of the right shoulder and some surface features of the transverse ridge. *Prophyllocrinus* sp. 3 differs from *P.* sp. 1 and *P.* sp. 2 by the coarse granular ornament. The specimen is probably a juvenile and with growth would have a facet much like that of *P.* sp. 1 or *P.* sp. 2.

**Sagenocrinitid** indet.
(Fig. 22D)

MATERIAL. QMF38896 from QML1233.

REMARKS. A weathered, poorly preserved, partial crown of an indeterminate sagenocrinitid shows part of the cup plates, part of one ray including an interbrachial series of 2 plates, and distal brachials of 2 or 3 rays. Critical parts of the cup, if preserved are not exposed to identify the genus. This is the first crown of a sagenocrinitid reported from the Callytharra Formation. It is illustrated to show the faunal diversity.

Loose flexible ossicles perhaps belonging to this taxon, are uncommon in bulk samples of the Callytharra Formation from the type section. Both cup and arm ossicles are present and the brachials show well-developed patelloid processes.

Subclass ARTICULATA Zittel, 1879

The Articulata is revised to include 8 orders, 7 as in the Treatise (Moore & Teichert, 1978) plus Ampelocrinida below. Articulata are characterised by brachial pairs with alternating muscular and cryptosyzygial articulation.

Order AMPELOCRINIDA ord. nov.

REMARKS. The Ampelocrinida (Table 2) includes Corythocrinidae, Tribrachyocrinidae, Calceolispongiidae, Ampelocrinidae (as constituted below) and the unassigned *Tasmanocrinus*. It may be defined as Palaeozoic genera not previously included in the Articulata but with brachial pairs with alternating muscular and cryptosyzygial articulation and lacking perfect pentameral symmetry.

Family AMPELOCRINIDAE Kirk, 1942

DIAGNOSIS. Cup bowl-shaped to discoidal, small; infrabasals small, subhorizontal to downflaring, commonly not visible in lateral view; 1 anal (exception, 3 in *Ampelocrinus*); radial facets plenary; arms commonly 10, rarely more, 2 primibrachs (exception, 3-4 in *Halogetocrinus*); isotomous branching; cuneate pinnulate brachials ; brachial pairs with alternating muscular and cryptosyzygial articulation; short anal tube where known (exception, recurved in *Ampelocrinus*); proximal stem commonly pentagonal or subpentagonal, rarely circular, in transverse section; very cirriferous close to cup where known.

GENERA INCLUDED. *Ampelocrinus*, *Chlidonocrinus*, *Cymbiocrinus*, *Halogetocrinus*, *Moundocrinus*, *Oklahomacrinus*.

REMARKS. Some species assigned to these genera may not belong to the Ampelocrinidae but a review of them is beyond the scope of this study. Genera assigned to the Ampelocrinidae by Moore et al. (in Moore & Teichert 1978), here excluded are *Arroyocrinus*, *Polusocrinus*,

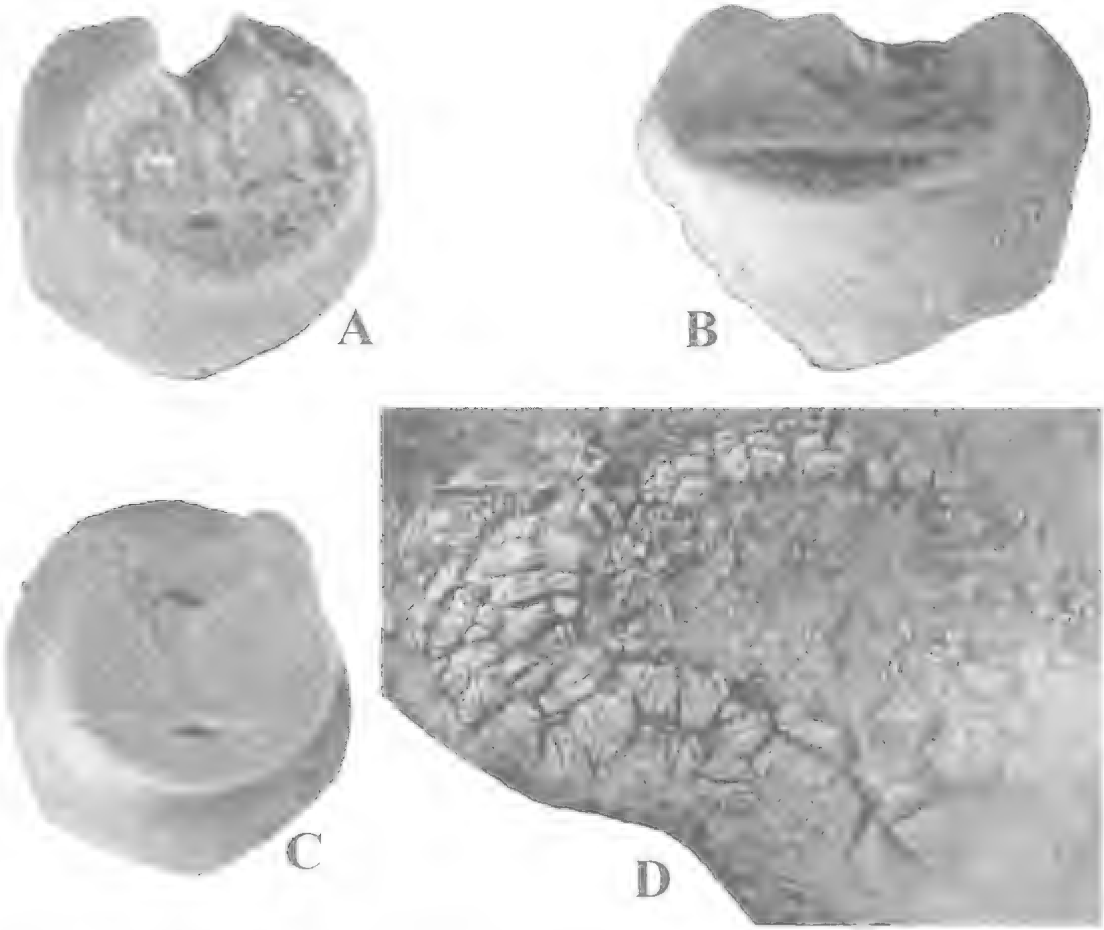


FIG. 22. A, *Loxocrinus* sp. 1, lateral view of radial QMF38889, ×9.4. B,C, *Loxocrinus* sp. 2. B, lateral view of radial QMF38890, ×5.8. C, lateral view of radial QMF38891, ×5.8. D, Sagenocrinitid indet., lateral view of weathered crown QMF38896, ×1.7.

*Proampelocrinus*, *Spheniscocrinus*, because they lack the brachial pairs with alternating muscular and cryptosyzygial articulation. Inclusion of some cymbiocrinids within and exclusion of some ampelocrinids from the Ampelocrinidae requires revision of both families, a revision beyond the scope of this paper. Ampelocrinidae are intermediate to upper tier feeders, adapted to carbonate or clastic substrates in equatorial latitudes.

## Family CALCEOLISPONGIIDAE Teichert, 1954

DIAGNOSIS. Bowl-shaped to cylindrical cup; thick plates; basals often extended as prongs or spines; 1 anal; radial facets plenary; arms 5 or more; 2 primibrachs if arms not atomous; isotomous branching; brachials cuneate; brachial pairs with alternating muscular and cryptosyzygial articulation; pinnulate; arms incurling distally when enclosed; no tegmen; stem subpentagonal or pentagonal proximally, commonly becoming circular distally; cirriferous near cup where known.

GENERA INCLUDED. *Calceolispongia*, *Allosocrinus*, *Jimbacrinus*, *Metacalceolispongia* gen. nov.

REMARKS. The calceolispongiids are best characterised by their thick plates, bowl-shaped or cylindrical cup, often with extended prongs on the basals and distally incurled arms. They are a bottom or very low tier feeding animal adapted to a carbonate or clastic environment in equatorial and higher latitudes.

**Calceolispongia** Etheridge, 1915

TYPE SPECIES. *Calceolispongia hindei* Etheridge, 1915 from the late Artinskian upper Noonkanbah Formation, Canning Basin, WA; by monotypy.

REMARKS. Two major papers by Teichert (1949) and Willink (1979b) described most of the 22 species of *Calceolispongia* from Australia. Teichert (1949) described 12 species from Western Australia and demonstrated their stratigraphic value in the Carnarvon and Canning Basins. He reported that one of the major evolutionary trends of the genus was towards enlargement of the basals which were used for resting on, or anchoring within, the substrate in adult stages. The stem of these forms was a tether in the immature stages and so small as to be of no or little functional value in the adult stage (Webster,1990). Willink (1979b) described 7 species, reassigned 2 species questionably assigned to *Phialocrinus* by Etheridge (1892) to *Calceolispongia*, and proposed an evolutionary lineage for the E Australian taxa. He based his lineage largely on the basals and 2nd brachials. Although E Australian species include forms with nodose ornamented or thick, slightly to moderately enlarged bulbous basals, they never developed the extremely enlarged bulbous basals typical of the youngest WA species. The oldest WA species are quite small and have slightly to moderately enlarged basals (Teichert, 1949).

Willink (1979b) considered that E Australian species evolved separately from the WA species. The earliest forms of both E Australian and WA lineages began in the Sakmarian. It is of more than passing interest that the 8 non Australian taxa of *Calceolispongia*, known from the Basleo deposits of Timor (Wanner, 1916, 1924, 1937; Marez-Oyens, 1940), and 1 from the Artinskian deposits of peninsular India (Reed, 1928) are all the greatly enlarged basal type. This suggests that the WA, Indian and Timor forms all developed in an interconnected area of the Tethys and were geographically isolated from the E Australian taxa.

Willink (1979b) also described in detail the brachial muscle and ligament structure and proposed a 2 dimensional rheophilic feeding fan for species of *Calceolispongia* with only slightly to moderately enlarged bulbous basals. This was based on a stemmed form supposedly elevated off the substrate. He compared the arms to some modern crinoids noting their similarity of brachial and muscle structure. This same basic arm structure is present, where known, on all species of *Calceolispongia*, whether the cup is a greatly enlarged or slightly to moderately enlarged basal form. This implies that the feeding strategy of the greatly enlarged basal cup form, living on or partially buried within the substrate, and the slightly to moderately enlarged basal cup form, elevated off the substrate by the stem, was the same. We suggest that the slightly to moderately enlarged basal form was not elevated significantly above the substrate. Instead we interpret it to have had a runner-like stem, with the proximal end upturned so that the cup was in a position very similar to, but perhaps slightly higher than, the cup with a vestigal tether stem. The slightly to moderately enlarged and nodose basals of the stemmed form helped hold the cup in an upright or inclined position, preventing overturning and fouling of the arms in the substrate.

The 2nd brachial, where known, of all species of *Calceolispongia* has protruded nodes to short blunt spines or coarse irregular ridges. This includes the extremely enlarged or slightly to moderately enlarged basal forms of the taxon. Willink (1979b) suggested that these enlarged brachials: 1, added weight to the crown enabling the cup to orient on its side in slower currents; 2, acted as stabilisers if the crown was suddenly bent in strong currents or detached and oriented on it side; and 3, would have produced considerable enhancing eddying particulate feeding when the cup was oriented horizontally.

We agree with Willink's analysis of the plate, muscle, and ligament structure of the arms of the calceolispongiids, but, in part, question the functional significance of the nodes, blunt spines, or irregular ridges on the 2nd brachial and feeding model. The added plate material of the enlarged 2nd brachial to the overall weight of the crown would be minimal, as they account for a small percentage of the overall bulk of the crown. In a detached crown the nodes or blunt spines could serve to stabilise the crown by projecting into the substrate, but this would normally require the 2nd brachials of 2 rays. With the nodes protruded into the sediment it would severely limit, if not completely negate, the function of the rest of those 2 arms, limiting the filtration fan to 3 rays. In soft sediment the base of the ambulacral trackways would probably be fouled by burial in sediment.

It is very doubtful that the crown commonly survived if detached from the stem. Autotomy of the stalk of Palaeozoic crinoids has been discussed by Donovan (1993) and Baumiller (1997).

Although the ability to autotomise the stalk developed in late Palaeozoic cladids (*Paragassizocrinus*, Webster & Lane, 1970; among others), it has not been demonstrated that other taxa could regenerate the distal stem and reattach. If they autotomised the distal parts of the stem and then grew additional stem proximally, living by grasping or burial attachment of the cirri, it should be recognised by finding a stem preserved with the cirri in the grasping or burial position and the distal end autotomised. The only regenerated stems reported from the late Palaeozoic are those of a flexible crinoid (Strimple & Frest, 1979) and *Lichenocrinus* (Ausich & Baumiller, 1993).

Use of the nodes or spines to produce eddy currents useful for feeding is considered minimal. Because the arms project outwards away from the cup into the current, only the proximal part of the arms could have benefitted if the calceolispongiids fed in a 2 dimensional or normal parabolic filtration fan posture.

The projections on the 2nd brachial of both greatly enlarged and slightly to moderately enlarged basal cups suggest that they served a vital function necessary to either a stemmed existence with the cup barely elevated above the substrate (slightly to moderately enlarged basals, runner type stem) or the cup resting on, or partly buried within, the substrate (greatly enlarged basals, stem vestigal in mature forms). We suggest that the nodes or blunt spines served a dual purpose, as stops and protection, and that the feeding posture was similar in both types of calceolispongiid cup.

As stops, the nodes and spines prevented the continued rotational movement of the arms as they opened to feed. On forms with the basals buried within the sediment the nodes or spines could have stopped against the sediment or abut against another organism living in close proximity. The first brachial on *C. abundans* had to rotate outward 76° from a vertical position for the nodes on the brachial above the outer ligament pit to stop against the distal tip of the radial external to the ligament pit on the radial facet. The nodes or spines of the 2nd brachial would have to rotate 135° to abut against the proximal parts of the radials and distal parts of the brachials. With the immovable ligamentary articulation between the 1st and 2nd brachials (Willink, 1979b) it is impossible for the nodes or spines to abut the cup plates. However, they could abut against adjacent organisms and deter predators nipping at the base of the arms in cups with the basals resting on the substrate or cups barely elevated above the substrate on a runner stem. In either of these positions the proximal brachials would be elevated above the substrate and the arms spread in a narrow to widespread filtration fan or they could have spread into a subhorizontal feeding position with pinnules elevated into the current.

Teichert (1949, pl. 8, fig. 2) illustrated the oral view of a crown of *C. abundans* with the proximal part of the enrolled portion of the arms unrolled along the bedding surface. The first 2 brachials are buried in the sediment at a high angle to the more distal brachials, with only the distal part of the 2nd brachial partly visible at the base of the arms. The cup is completely buried. We interpret this specimen to have been in the feeding posture at the time of rapid burial followed by death. If the specimen died before burial, any current (such as that necessary to bury the specimen in sand) would have moved the arms into a semi-aligned postion, if not broken them off. This suggests that the enlarged basal calceolispongiid species, with the cup resting on or buried within the sediment, fed with the arms extended along the substrate rather than above the substrate up in the current in a 2 dimensional or normal parabolic filtration fan posture. The enrolled arms in the nonfeeding position prevented sediment from fouling the inactive ambulacral trackways and removed the arms from the paths of predators and benthic scavengers.

This also explains the relatively large space in the muscle area between the radial and 1st brachial facets (Willink, 1979b, fig 11) in the relaxed and flexed positions. Most cladid crinoids have relatively small spaces between the radial and 1st brachial facets when closed (muscle contracted) and larger spaces when open (muscle relaxed), because the muscle area of the radial facet is subhorizontal. The facet of the radial is steeply downflared into the cup of *Calceolispongia*, while the brachial facet is subhorizontal with the arm in the enrolled contracted position, not the relaxed position as shown by Willink. In the relaxed position the arm is unrolled and extended out into the feeding position with the ligament in the outer ligament pits of the radial and 1st brachial contracted. In both conditions the cross-sectional area between the muscle areas of the facets is relatively larger than in most poteriocrininids.

When closed the arms of the calceolispongiids

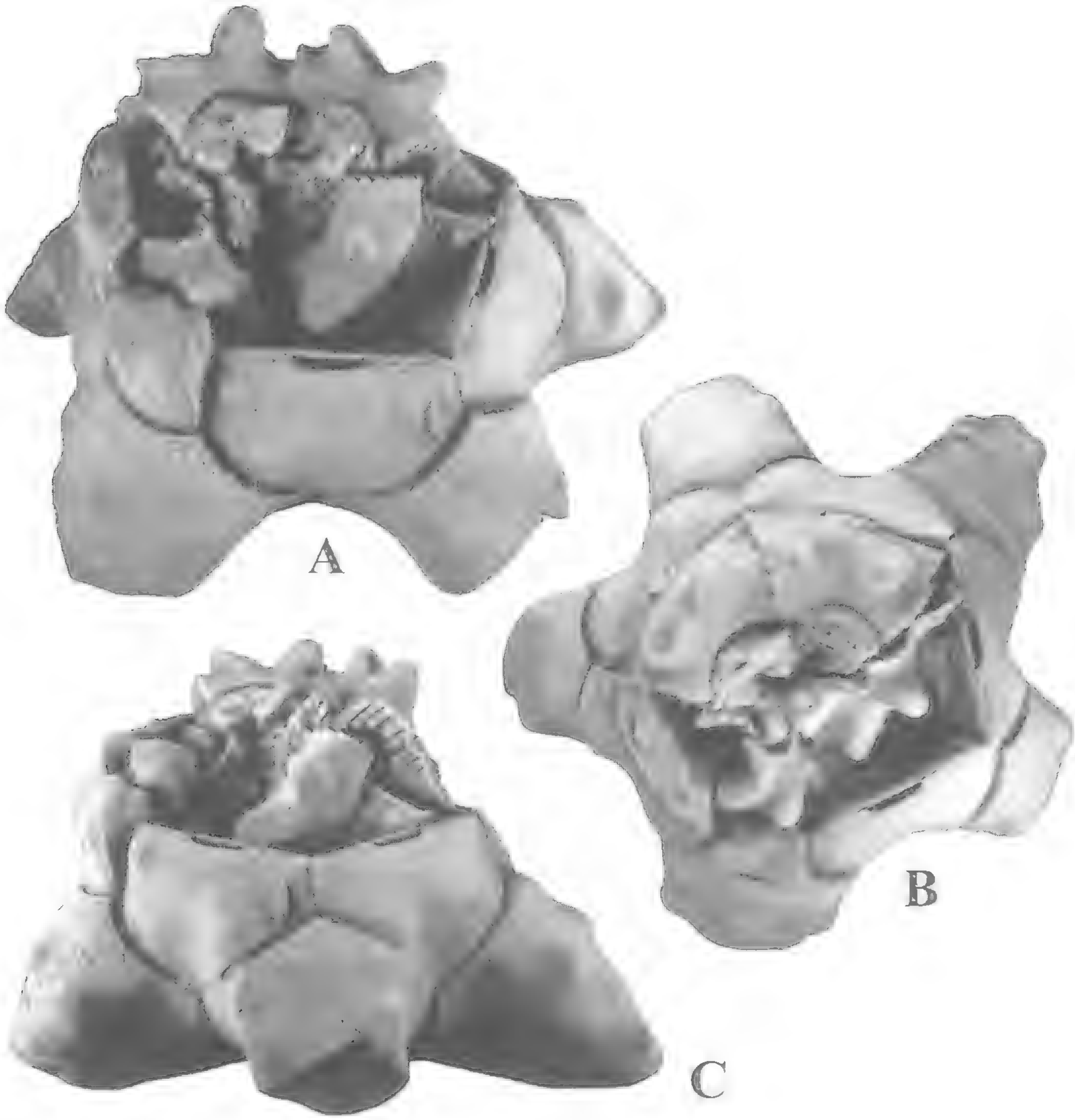



FIG. 23. *Calceolispongia abundans* Teichert, 1949, oblique C ray (A), distal (B) and B-C interray (C) views of partial crown QMF38874, ×2.3.

formed an open pentagonal petaloid structure in distal view, not the tightly enclosed crown of most poteriocrininids. However, the 1st and 2nd brachials were more tightly enclosed, surrounding the visceral mass protruded above the radial summit in the tegmen. The base of the enrolled arms formed a constriction, the arm girdle (Lane & Webster, 1966), above the 2nd brachial.

Another use of the node or spines on the 2nd brachial could have been to deter settlers from using the shelf developed atop the 2nd brachial and deny predators access to the visceral mass.

**Calceolispongia abundans** Teichert, 1949
(Figs 23, 24A-C)

MATERIAL. QMF38874 from QML1217.

REMARKS. The partial crown, an immature specimen (24mm long, 33mm maximum width), lacks the stem, tips of the protruded part of 4 basals and all distal parts of the arms beyond the

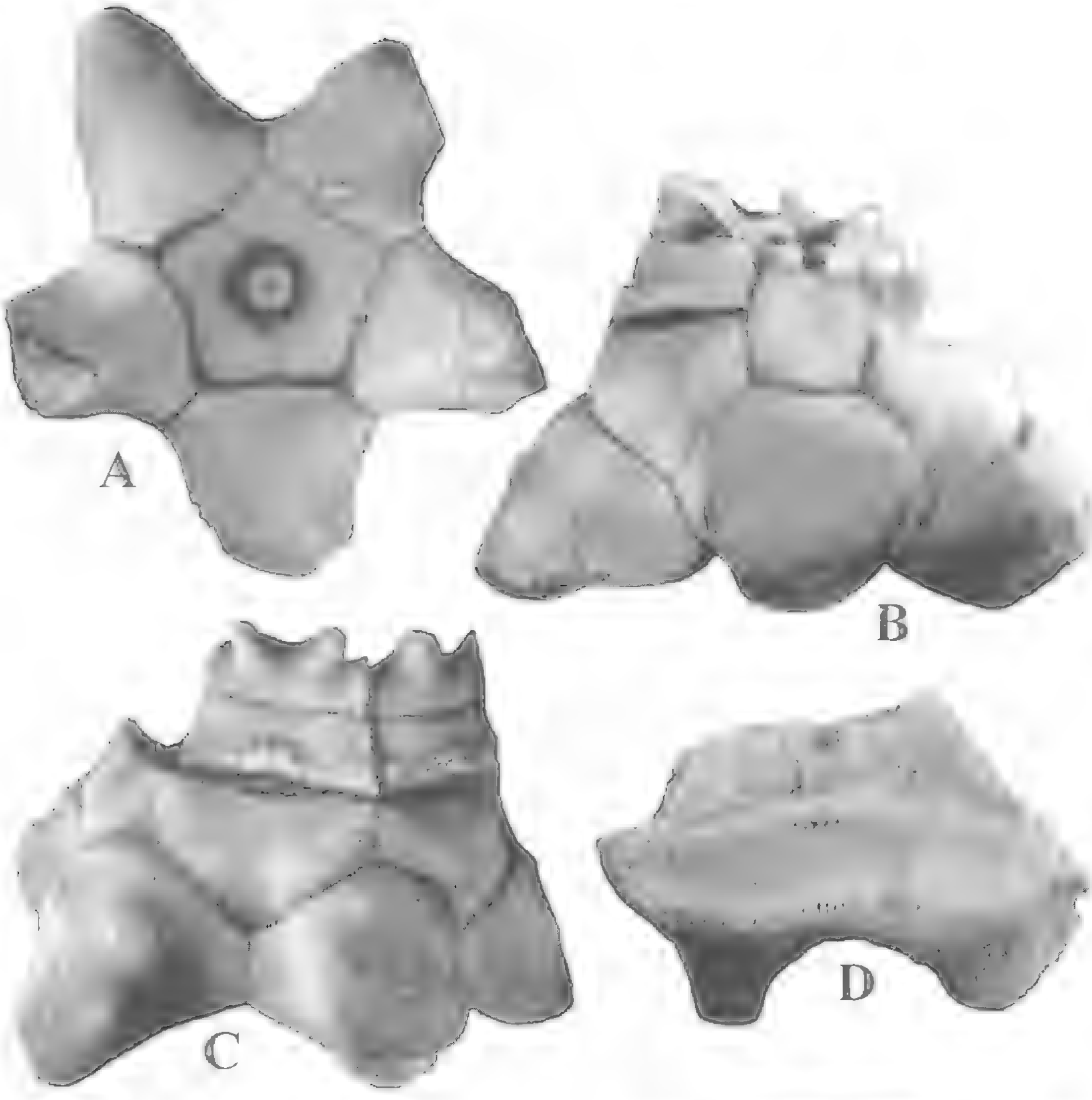




FIG. 24. A-C, *Calceolispongia abundans* Teichert, 1949, basal, posterior and A ray views of partial crown QMF38874, ×2.3. D,E, *Calceolispongia rubra* Teichert, 1949, proximal and distal facet views of 2nd brachial QMF38876, ×4.1.

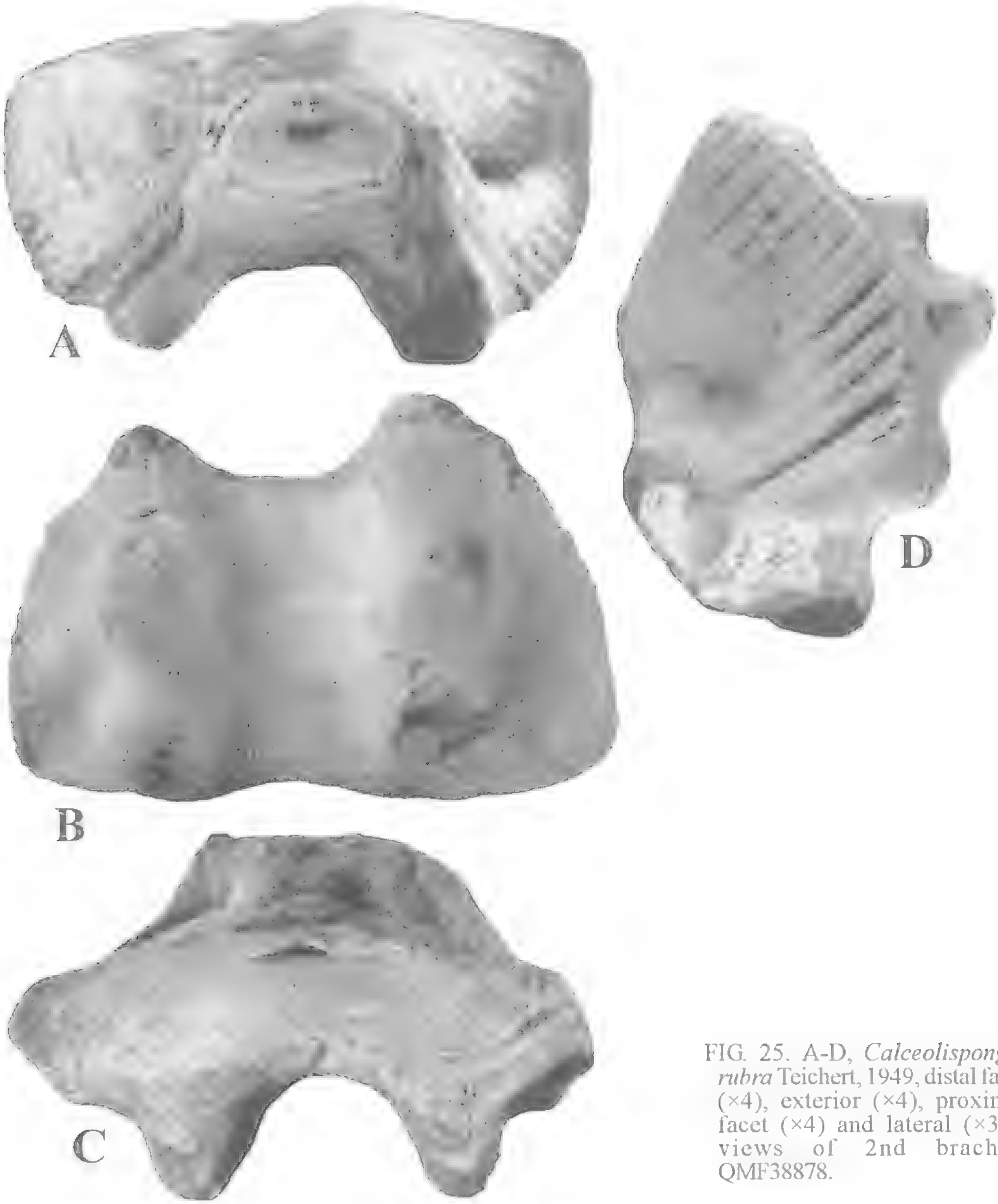


FIG. 25. A-D, *Calceolispongia rubra* Teichert, 1949, distal facet (×4), exterior (×4), proximal facet (×4) and lateral (×3.2) views of 2nd brachial QMF38878.

4th brachial. It was transported to the site of burial with loss of the stem and perhaps some of the distal parts of the arms. At the site of deposition some of the 1st to 4th brachials were disarticulated and moved into the visceral cavity as the specimen was buried. The silt and sand enclosing the partial crown and the associated disarticulated plates are compacted and slightly cemented. Most of the enclosing matrix is easily removed by wetting, brushing with a moderately stiff tooth brush and light scraping with a needle under the microscope.

Features not previously described on *C. abundans* are the ridges and grooves of the lateral ends of the 1st and 2nd brachials. The 1st ridge and groove are 1.7mm above the proximal end of the 1st brachial and the last is at the distal end of the 2nd brachial. Initial ridges and grooves are

short and of low amplitude, whereas distal ones have higher amplitude. With the brachial in a living or near vertical position, the ridges and grooves are oriented nearly horizontally with a very gentle curvature, centrally convex upward. There are 7 ridges on the 1st brachial in 2.8mm, and 6 ridges in 2.7mm on the 2nd brachial. In lateral view, with the arms enclosed, they appear to interlock with false symplectic articulation.

Development of the ridges and grooves on the ends of the proximal brachials is known in other species of *Calceolispongia*, such as *C. lizziensis* (Willink, 1979b, pl. 9, fig. 18) and *C. spectabilis* (Teichert, 1949, pl. 19, fig. 40), as well as poterio-crinitoids such as *Spaniocrinus*, as described above. Most commonly the apparent interlocking occurs between apposing brachials and may extend along most of the arms of adjacent rays, such as in *Parastachyocrinus*. In these forms alternate brachials form the groove and ridges of 1 arm and the brachials of the adjacent arm form the counterparts to produce the interlocking fit. Webster & Lane (1967) referred to this as an 'interlocking structure' and interpreted it as adding strength to the enclosed crown. They also considered that this limited the movement of the proximal brachials below the arm girdle or constriction in the arms occurring immediately above the interlocking on the cromyocrinid *Moapacrinus*. The interlocking of adjacent brachials is structurally quite different from the ridge and groove development on individual brachials of *Calceolispongia*, although they may have served a similar purpose.

We suggest the structures in the calceolispongiids served as sliding guides for differential rotational movement of adjacent proximal brachials as the arms were opening and closing as well as guides for forming a close fit when the arms were entirely extended and were being tightly enclosed. A rotational movement of the arms above the transverse ridge of the radial facet occurred as the arms opened and closed. Thus gently curved ridges and grooves allowed a relatively smooth differential movement between laterally adjacent plates. The crinoid could flex 1 arm to a greater or lesser degree than the 2 adjacent arms. When the arms are flexed to a position where the 1st and 2nd brachials were not in lateral contact with the brachials of adjacent rays (Teichert, 1949, pl. 9, figs 1, 2), the ridges and grooves of one arm were not in contact with those of adjacent rays, but would have served as guides for proper positioning of the brachials as the arms enclosed.

In the enclosed position the ridges and grooves would have also restricted translational movement of the 2 proximal brachials parallel to the long axis of the arms. This would allow tensional forces (such as predators nipping the tips of the arms or accidentally hitting the arms while chasing prey) applied to the distal parts of the arms to be mitigated by the added strength of the 2 adjacent arms on the proximal 2 largest brachials. Depending upon the amount of tension, this could have resulted in retention of the 2 proximal brachials, the largest in the arm, when the distal brachials were lost. Retention of the proximal part would require regeneration of fewer brachials and thus less time and energy to replace the lost part of the food gathering network.

The enlarged proximal 2 brachials surrounded an expanded visceral cavity. We suggest that they served as a plated structure surrounding the tegmen in the enclosed position, while also serving as moveable arm bases. To accomodate expansion of a full gut tract, the 2 proximal brachials would have rotated outward. The ridge and groove structure would have allowed smooth expansion and contraction with a slight rotational movement of the proximal brachials. The nodes or blunt spines on the 2nd brachial would have served for protection analogous to tegmen spines. In the feeding position, the opened arms would have allowed some exposure of the visceral mass above the radials, covered only by the tissue of the tegmen.

Teichert (1949) described the nervous system of *Calceolispongia* as a series of fine canals on the inner side of the cup plates. He did not mention the dual entoneural canals of the brachials. From the radials there are 4 canals that pass into the first brachial on the oral side of the transverse ridge of the arm facet. On the distal cryptosyzygial facet with the 2nd brachial the 4 canals continue into the inner side of the 2nd brachial and as they come out on the distal side they merge into 2 canals continuing throughout the more distal brachials. The 2 very small entoneural canals are on the oral side of the centre of the transverse ridge of facets with muscular articulation and at the growth centre of brachials with cryptosyzygial articulation. First and 2nd brachials (QMF38875-38878) of *C. rubra* Teichert, 1949 from the Wandagee Sandstone (QML1222) show the canals (Fig. 24D,E, 25, 26A-D). The dual internal canals also occur in the brachials of *Jimbacrinus bostocki*. In *J. bostocki* they pass across the radial facet into the 1st brachial on the oral side of the transverse ridge. In the distal

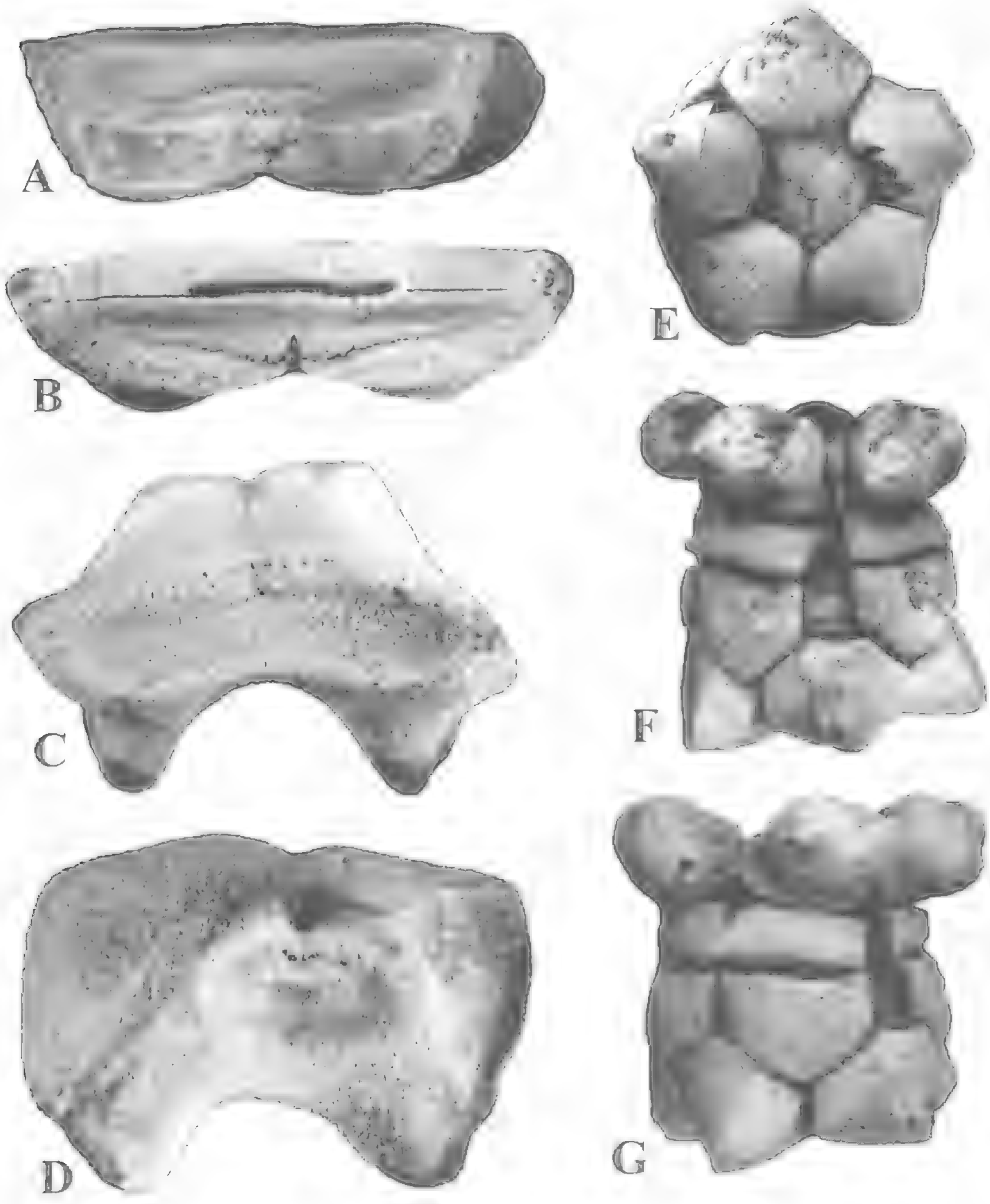



FIG. 26. A-D, *Calceolispongia rubra* Teichert, 1949. A,B, distal and proximal facet views of first brachial QMF38875, ×4.1. C,D, proximal and distal facet views of second brachial QMF38877, ×4.1. E-G, *Calceolispongia gerthi* Willink, 1979b, basal, posterior and D ray views of reconstructed crown GSQF13488, ×1.5.

brachials thereafter, there are dual canals as in *Calceolispongia*.

**Calceolispongia gerthi** Willink, 1979b
(Fig. 26E-G)

MATERIAL. GSQF13488a-r, 5 basals (13488a-e), 5 radials (13488f-j), 4 first brachials (13488k-n), and 4 second brachials (13488o-r) from the early Artinskian Berridale Formation, Rathbone's Quarry, Granton, Tasmania. Collected by S. Parfrey.

REMARKS. Willink (1979b) based the description of *Calceolispongia gerthi* on disarticulated second brachials. He recognised that the basals were not distinguishable from those of *C. diemenensis* and described and illustrated basals referred to as *C. gerthi-diemenensis*. No cups or crowns were reported for either species. All of the material came from the Crinoidal Zone on Maria Island.

The discovery of disarticulated plates from a single specimen in a thin shale between 2 limestone layers in the Berridale Limestone allowed the reconstructon of a partial crown including the first 2 brachials. Among the 5 basals, only the CD basal has a truncated distal end for reception of the anal plate, which was not recovered. Under the microscope the sutures of the basal and radial plates along the anal interseries were shorter than those between comparable plates in other interrays. Likewise, facets between the radials and 1st brachials of the C and D rays were shorter than those in other rays, and had a short gap on the end adjacent to the anal interray, allowing recognition of their positions within the cup. Facets of the 1st and 2nd brachials of the C and D rays were shorter and slightly twisted compared to those in other rays allowing easy recognition. The rest of the specimen was reconstructed around the C and D rays. The BC and DE basals are broken, but the pieces were glued together. Unfortunately the BC basal was also distorted by compaction and the DE basal was solution weathered. It is uncertain if they are in the correct positions or interchanged on the reconstruction. The AB and EA basals would not fit the sutures for the BC and DE, and are thus presumed to be in their correct positions. The third 1st brachial could fit on the E, A, or B radials, and thus its position, though correct within a ray, cannot be more precise. Likewise the 2 second brachials have been solution weathered and it is uncertain which, if either, fit the 1st brachial. The infrabasal circlet was not recovered.

The reconstructed partial crown is cylindrical and probably rested on the enlarged basals on the substrate with a runner or tether stem. The proximal side of the blunt spine projections is essentially horizontal, and the infrabasal circlet is not visible in side view, as it is downflaring or subhorizontal and confined to a shallow basal concavity. The radials are subvertical and the protruded knobs of the 2nd brachials are subhorizontal to slightly upflared in the enclosed position. When the arms were fully extended laterally the knobs would have rested against the apex area of the subjacent radial and 2 basals.

If *C. gerthi* lived elevated slightly above the substrate, the basal projections could have served as bumpers to keep the crown in a near upright position when tilted by currents or scavengers. The blunt spines on the basals along with the knobs of the 2nd brachials would help to prevent the arms getting into the sediment and ambulacral trackways from getting fouled when hit by scavengers or strong current surges. From the shape of the reconstructed cup it is most likely that *C. gerthi* rested on the substrate with a runner stem.

**Calceolispongia** sp.
(Fig. 27)

MATERIAL. One slab with 3 basals, anal, and numerous brachials, all external moulds, QMF39012 from QML518.

DESCRIPTION. Plates thickened, basals protruded into short double spine projecting out and upward, surface ornament coarse nodes and anastomosing ridges aligned towards spine tips. Anal pentagonal, with central rounded node. Brachials cuneate, concave longitudinally, strongly rounded transversely; ambulacral groove wide, deep V-shaped.

REMARKS. The plates of *Calceolispongia* sp. are part of a single specimen disarticulated by currents or scavengers leaving them in close association. Other plates are unknown, either not exposed or lost by weathering. The basals are similar in shape to *C. gerthi* and *C. diemenensis* (Willink, 1979b), except they have surface ornament in addition to the double spine. If these plates are from a fully grown individual, the specimen would have been small, cylindrical, and lived on the substrate with a runner stem. It probably represents a new species, based on the nodose to anastamosing ridge ornament, that evolved from *C. gerthi* or *C. diemenensis*. Lacking radials and proximal brachials it is left in open nomenclature and mentioned for completeness of the Condamine fauna.

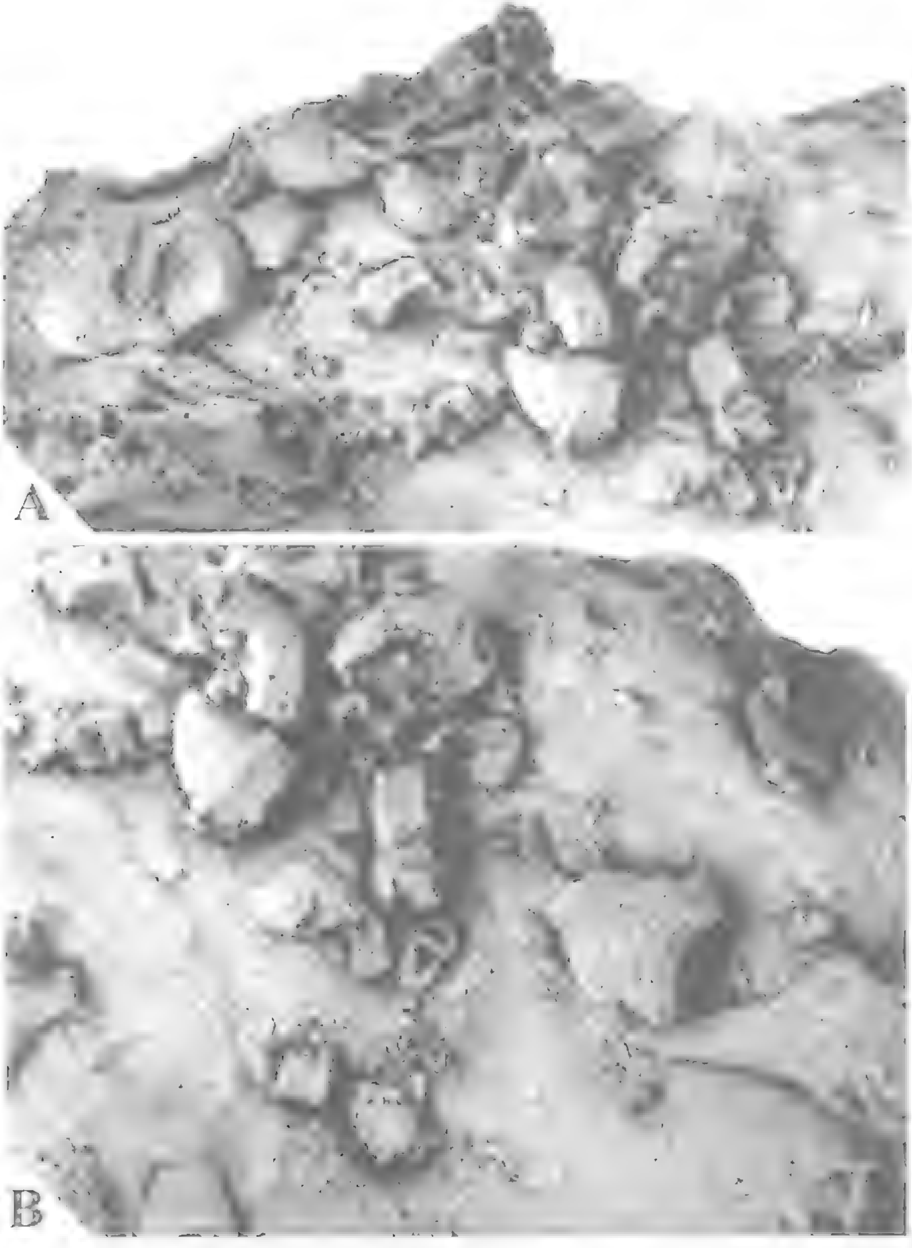



FIG. 27. *Calceolispongia* sp., overlapping views of dislocated cup and arm plates, QMF39012, ×2.5.

**Jimbacrinus** Teichert, 1954

TYPE SPECIES. *Jimbacrinus bostocki* Teichert, 1954, from the Artinskian Cundlego Sandstone of WA; by original designation.

**Jimbacrinus donnellyensis**
Webster & Jell, 1992

*Jimbacrinus donnellyensis* Webster & Jell, 1992: 353, fig. 21.

REMARKS. The locality for *J. donnellyensis* was given as from the upper part of the Artinskian Bulgadoo Formation in the type section near Donnelly's Well (Webster & Jell, 1992). Because this is one of the few limestone environments above the Callytharra Formation in the Permian of WA the locality was deemed worthy of reinvestigation for additional information and

more precise location. The yellow weathering limestone is a small lense, forming a weak bench at the base of the slope, QML1141. Collection yielded 45 crowns of *J. donnellyensis* (QMF39151-39195), 3 crowns of *Stomiocrinus merlinleighensis* (QMF39196-39198), 7 basals of *Calceolispongia* sp. (QMF39210-39216), 8 columnals of *Neocamptocrinus* sp. (QMF39202-39209), 2 radials of *Thaumatoblastus* sp. (QMF-39200, 39201) and 1 spine of *Archaeocidaris*? sp. (QMF39199). All specimens are in loose blocks or occur as free elements.

**Metacalceolispongia** gen. nov.

TYPE SPECIES. *Cymbiocrinus cherrabunensis* Webster & Jell, 1992 from the Wuchiapingian Cherrabun Member, Hardman Formation, WA.

ETYMOLOGY. Greek *meta*, between or change, and *Calceolispongia*, implying a derived form.

DIAGNOSIS. Bowl-shaped cup, thick inflated plates, apical pits, 1 anal, plenary radial facets, 2 primibrachs, 11 arms minimal incurl distally, brachials cuneate, muscular and cryptosyzygial paired brachials, pentagonal proximal columnals.

REMARKS. *Metacalceolispongia* differs from all other calceolispongiids by having more than 5 arms. It is similar to *Cymbiocrinus*, differing by having more than 10 arms, thick plates and a pentagonal stem proximally. It could have evolved from *Allosocrinus* by further branching of the arms or from *Calceolispongia* by branching of the arms and less protrusion of the basals.

**Metacalceolispongia cherrabunensis**
(Webster & Jell, 1992)

*Cymbiocrinus cherrabunensis* Webster & Jell, 1992:351, fig. 20.

DESCRIPTION. See description of *Cymbiocrinus cherrabunensis* Webster & Jell (1992: 351).

REMARKS. Webster & Jell (1992) commented that the 3rd arm on the C ray of *C. cherrabunensis* is atypical of *Cymbiocrinus* and noted the affinities to *Jimbacrinus*. Evaluation of *Cymbiocrinus* and the Calceolispongiidae within the Articulata lineage resulted in reassignment.

Family TRIBRACHYOCRINIDAE
Arendt & Willink, 1981

DIAGNOSIS. Cup globose, relatively large; infrabasals upflared, distal tips visible in lateral view; radial facets plenary; 1-4 anals; 12 or 20 arms; isotomously branching; cuneate brachials ramulate; brachial pairs with alternating muscular and cryptosyzygial articulation; stem relatively large, round in transverse section, with round lumen; may be very cirriferous close to cup.

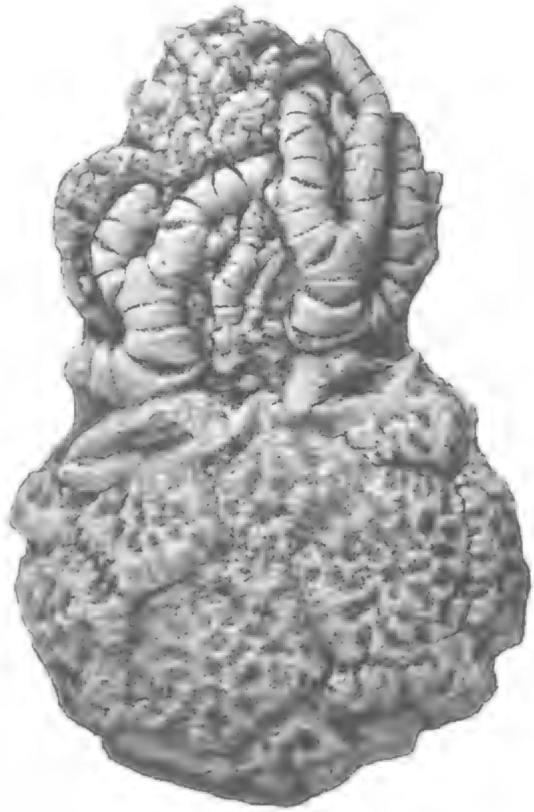


FIG. 28. *Tribrachyocrinus corrugatus* Ratte, 1885, B ray view of crown Z3256, ×2.3.

GENERA INCLUDED. *Tribrachyocrinus*, *Meganotocrinus* and *Nowracrinus*.

REMARKS. *Tribrachyocrinus* was assigned to the Sundacrinidae on the basis of arms developed in 3 rays (Moore & Laudon, 1943) and made the monotypic type of the Tribrachyocrinidae by Arendt & Willink (in Arendt, 1981). *Meganotocrinus* was questionably assigned to the Ampelocrinidae and *Nowracrinus* was considered incertae sedis (Willink, 1979b). Except for the non-development of arms in 2 rays and a larger number of anals there is little difference between *Tribrachyocrinus* and *Meganotocrinus* or *Nowracrinus*. *Nowracrinus* differs from *Meganotocrinus* by stellate crenulations extending across plate boundaries. The tribrachyocrinids differ from all other Ampelocrinida by the development of ramules instead of pinnules and the large transversely circular stem. They were an

intermediate or upper tier feeder, adapted to carbonate and clastic substrates in higher latitudes.

**Tribrachyocrinus** M'Coy, 1847

TYPE SPECIES. *Tribrachyocrinus clarkii* M'Coy, 1847 from Roadian or Wordian sediments in the Maitland district, NSW; by original designation.

**Tribrachyocrinus corrugatus** Ratte, 1885
(Fig. 28)

MATERIAL. TMZ3256, from the Malbina Formation, late Artinskian, Storm Bay Sheet 8411, 1:100,000, grid reference 773 348, Tasmania. Collected by Andrew Rozefelds, Max Banks, and Noel Kemp.

DESCRIPTION. Crown small, 42mm long, 26.6mm wide, all cup plates with coarse corrugate ornament. Part of infrabasals, basals, A-C radials, radianal, 3rd anal, parts of A and C ray arms preserved in flattened plane. Radial facet plenary. First primibrach wedge-shaped, tapering distally. Axillary 2nd primibrach triangular, distal tip separating facets for widely diverging 1st secundibrachs. Axillary 2nd or 3rd secundibrach, shaped like axillary primibrachs. Both branchings isotomous. All distal brachials cuneate, uniserial, straight to weakly concave longitudinally, strongly convex transversely, with smooth external surface. Large ramule or small arm on every 2nd tertibrach, alternating sides of main arm for next 4-6 brachials, unknown thereafter. In A ray first ramule on 3rd tertibrach, 2nd ramule on 5th tertibrach on 1/2 ray adjacent to C ray. In 1/2 ray adjacent to D ray 1st ramule on 2nd tertibrach, 2nd ramule on 5th tertibrach. Thereafter ramules every other tertibrach. Brachials paired, musculature articulation on branching facets and after ramules alternating with cryptosyzygial.

REMARKS. The small crown is crushed by compaction. It is the first crown of this species known with well-preserved arms of 2 rays. The description of the arms supplements the excellent cup analysis and description of *T. corrugatus* by Willink (1979b).

**Tribrachyocrinus granulatus** Etheridge, 1892
(Fig. 29)

MATERIAL. TMZ3258, from the Malbina Formation, late Artinskian, Storm Bay Sheet 8411, 1:100,000, grid reference 773 348, Tasmania. Collected by A. Rozefelds, M. Banks and N. Kemp.

REMARKS. The cup has a 1.8mm diameter hole drilled through the left central part of the large A-C basal plate in the centre of the flattened specimen. Non-predatory drill holes in the tegmen plates of Early Carboniferous camerate crinoids were described by Baumiller (1990) and epizoan pits on cup, tegmen and arm plates of early and middle Palaeozoic crinoids were reported by Brett (1978, 1985). To our knowledge, no predatory drill holes through cup plates of Palaeozoic crinoids have been reported. The hole was there prior to deposition, is filled with the surrounding fine silty clay matrix and has a compaction fracture through the plate crossing the right edge of the hole. Burial was rapid as no overgrowths or abrasion occurred. Solution weathering has destroyed part of the surface calcite of most exposed plates. Scavengers have not disarticulated the cup plates and the degree of articulation of the parts of the arms present cannot be determined because of matrix cover. A small, gastropod, *Peruvispira* sp., 3.7cm away from the cup, is not known to be carnivorous (A. Cook, pers. comm., 1998) and is not thought to have been associated in a coprophagous relationship with the specimen.

FIG. 29. *Tribrachyocrinus granulatus* Etheridge, 1892. C ray view of cup with drill hole in radianal. Z3258, ×2.6

Willink (1979b) considered *T. granulatus* uninterpretable and recommended suppression

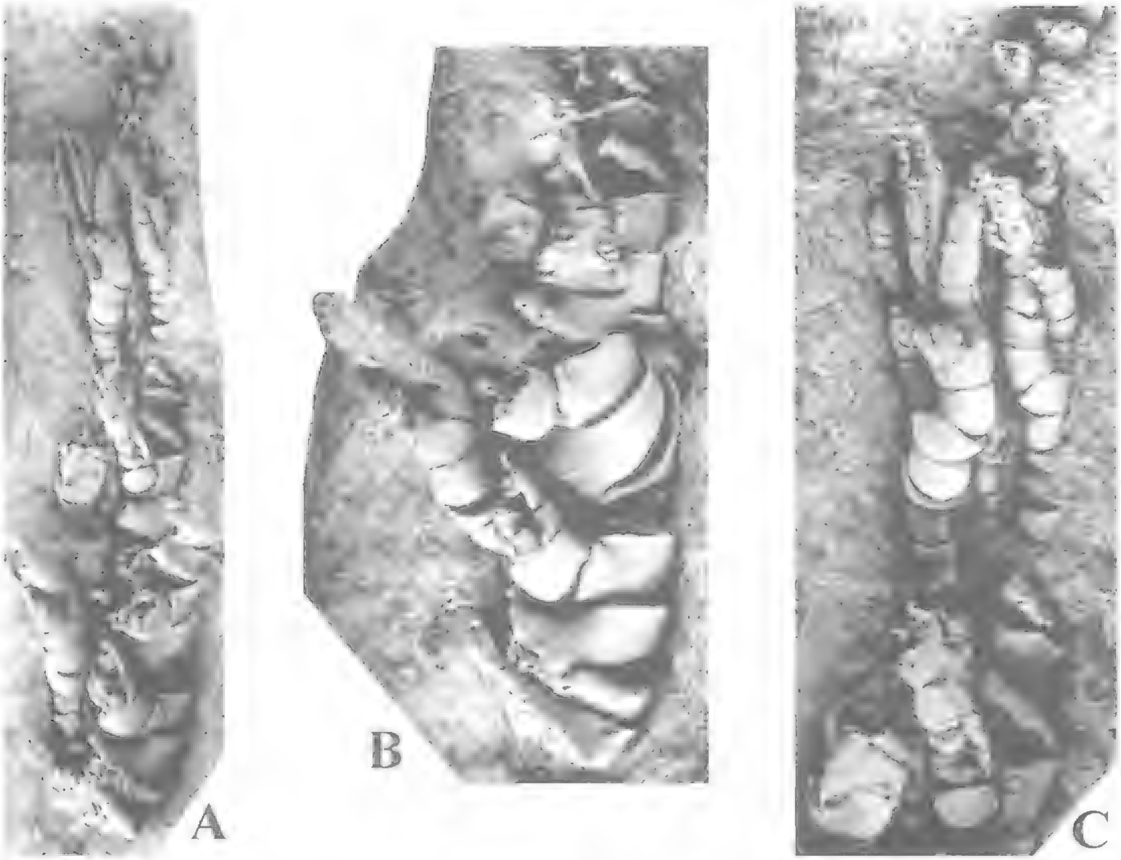


FIG. 30. *Tribrachyocrinus*? sp. arm fragment, A-C, lateral view of whole specimen (×1.7), enlarged proximal (×2.4) and distal (×3.1) views of QMF38898.

of the species because no additional material had been found. He also considered *T. granulatus* as possibly representative of *T. rattei* Willink, 1979. If such were proven *T. granulatus* would have precedence. *T. rattei* has aligned nodes coalescing into ridges. *T. granulatus* has only nodes, which may show alignment, therefore we accept both species.

**Tribrachyocrinus**? sp., arm fragment
(Fig. 30)

MATERIAL. QMF38898 from QML806.

DESCRIPTION. Arm large, 60mm long (incomplete), branching of indeterminate type on 6th brachial, may branch again distally. Brachials large, (proximal brachial 3.2mm long, 6.7mm wide, 7mm deep), uniserial, moderately cuneate, concave longitudinally, strongly convex transversely, large ramule given off on every other brachial on opposite sides of arm (2 ramules per 4 brachials). Articular facet of proximal brachial with large rounded transverse ridge; narrow crescent-shaped outer margin with deep ligament pit adjacent to transverse ridge; muscle areas large, narrowing distally. Ramulars moderately cuneate, straight to weakly convex longitudinally, strongly convex transversely. Ramules branching on ramular 4 or 5, may branch again on secundiramular 2, and tertiramular 2; may give off small unbranched ramules of pinnular size. Brachials paired with muscular articulation where branching or a ramule is given off alternating with cryptosyzygial articulation where no branching occurs.

REMARKS. The branching pattern of the ramules is similar to that of *Tribrachyocrinus corrugatus* above the branching on the second secundibrach. The branching of the ramules may represent a specific difference. The branching also resembles that of the Silurian flexible *Cholocrinus obesus* (Angelin, 1878), the Early

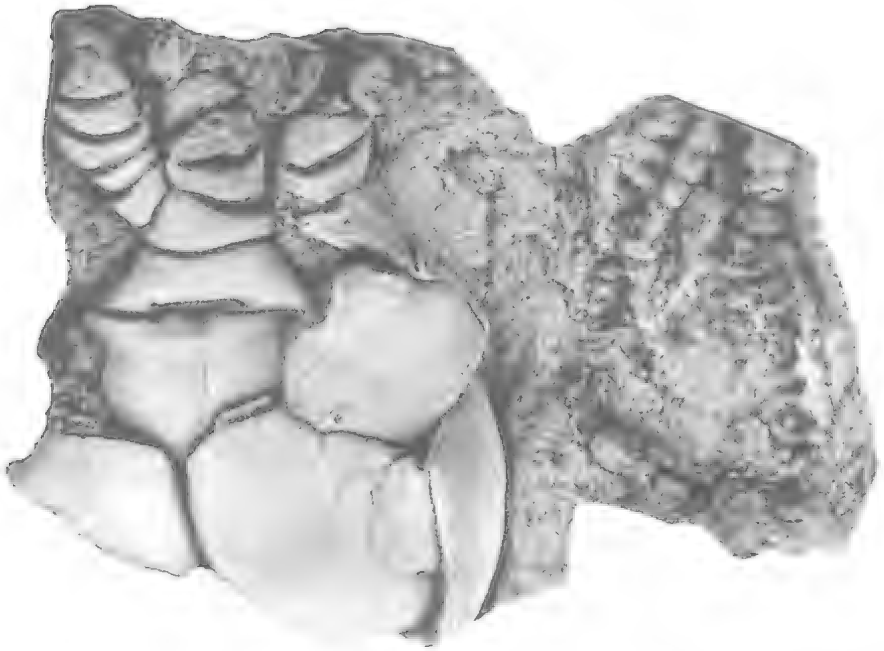


FIG. 31. *Meganotocrinus princeps* (Etheridge, 1892), lateral view of abnormal crown BME68151, ×1.7.

Carboniferous cyathocrinitid *Barycrinus asteriscus* Van Sant, 1964 and flexible *Onychocrinus exsculptus* Lyon & Casseday, 1860. There is no indication of patelloid processes on either brachials or ramulars and the articular facet of the 1st brachial is of a form common to many poteriocrinitids.

**Meganotocrinus** Willink, 1979

TYPE SPECIES. *Phialocrinus princeps* Etheridge, 1892 from Artinskian Muree Sandstone Member, Branxton Formation, NSW; by original designation.

**Meganotocrinus princeps** (Etheridge, 1892)
(Fig. 31)

MATERIAL. BME68151, Middle Permian, from an unknown locality in Queensland or NSW.

REMARKS. A request for loan of the type specimen of *Poteriocrinites smithi* resulted in not only the plasticine type of *P. smithi*, but, the external mould of a partial crown of *Meganotocrinus princeps* with an identification label of *P. smithi*, from the Gympie Beds, Stanwell, near Rockhampton. The specimen is part of the Dunstan Collection, purchased by the British Museum, July 1935. There is obviously a mixup in the locality and identification of the specimen.

This specimen of *M. princeps* is an external mould of parts of 3 rays of an abnormal cup and proximal brachials, with associated, but not attached, distal parts of 3 or 4 arms. It is embedded in a volcaniclastic matrix. Permian strata in the Stanwell area are the Early Permian Youlambie Conglomerate and early Late Permian Dinner Creek Conglomerate. Permian volcaniclastic deposits are present in and SE of the Rockhampton area, about 25-45km E of Stanwell. Other Permian volcaniclastics and sedimentary deposits are present 20-30km W and SW of Stanwell. Thus the specimen could be from the Stanwell or Rockhampton area. All reported localities of *M. princeps* are in NSW (Willink, 1979b).

The abnormality occurs on one of the radials, which lacks the development of the arm and terminates in a distally projected wide V-shaped extension. The 1st primibrachs of the 2 adjacent arms partly overlap the radial, the one on the right more than that on the left. There is no indication of a radial facet, nor of any injury. This appears similar to B and E radials in *Tribrachyocrinus* where no arm is developed. If the 3 basals were not exposed the specimen would have been assigned to *Tribrachyocrinus*. It is interpreted as a genetic defect and is illustrated to show the abnormality, but may also indicate the close

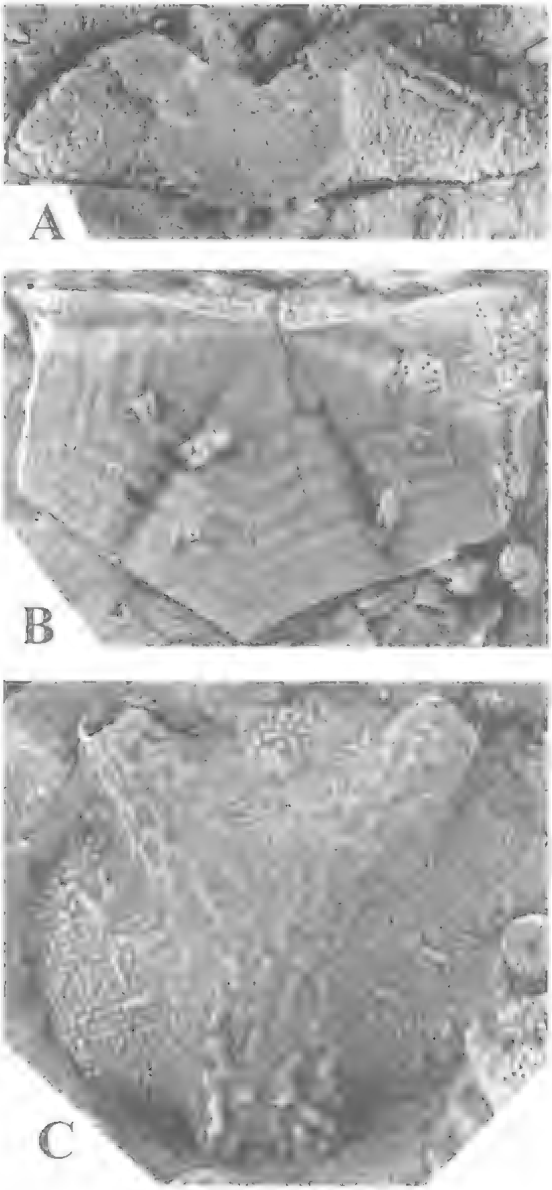


FIG. 32. *Nowracrinus ornatus* Willink, 1979. A, distal facet view of primibrachial QMF39020, ×2.8. B, internal view of radial QMF39015, ×2.4. C, external view of basal QMF39014, ×3.4.

relationship between *Tribrachyocrinus* and *Meganotocrinus*.

**Nowracrinus ornatus** (Etheridge, 1892)
(Figs 32, 33)

*Tribrachyocrinus ornatus* Etheridge, 1892: 94, pl. 19.
*Nowracrinus ornatus* (Etheridge); Willink, 1979a: 124, figs 3-6f.

MATERIAL. Basal, QMF39014, radial QMF39015 primibrachs, QMF39019, 39020 and columnals QMF39016-39018, 39021, 39076, 39077 from QML1247.

DESCRIPTION. This description only adds or alters that of Willink (1979a). Pluricolumnal heteromorphic, pentagonal in transverse section. Noditaxis N3231323 minimal, may be more complex. Columnals large, pentagonal nodal 10.1mm diameter, c. 1mm thick; internodals subround to pentagonal, weakly pentastellate, 8.5mm diameter, <0.7mm thick. Nodal latus narrow, strongly protruded, relatively sharp, rounded; internodal latus similar. Facets with narrow crenularium parallel to pentagonal sides of columnal, crenulae and culmina coarse, straight sided, slightly longer at angles of columnal, otherwise equal length. Areola narrower to slightly wider than crenularium. Lumen large, subcircular to pentagonal, parallel to outline of columnal. Symplexy articulation. Nodals with 5 cirri. Cirral facet elliptical, long axis parallel to columnal facets, with small central axial canal.

REMARKS. Combination of the intraplate crenulations and nodose to vermiform ornamentation are the distinctive features of cup plates of *N. ornatus*. Columnals lack surface ornament but the pentagonal and pentastellate outline combined with distinctive facets could be used for correlation in absence of the cup plates. All columnals are slightly to moderately distorted from compaction.

Family INCERTAE SEDIS

**Tasmanocrinus** Willink, 1979

TYPE SPECIES. *Tasmanocrinus mariensis* Willink, 1979, from Sakmarian strata on Maria Island, Tasmania; by original designation.

**Tasmanocrinus** sp.
(Fig. 34)

MATERIAL. TMZ3259, from the Malbina Formation, late Artinskian, Storm Bay Sheet 8411, 1:100,000, grid reference 773 348, Tasmania. Collected by Andrew Rozefelds, Max Banks, and Noel Kemp.

DESCRIPTION. Crown cylindrical, 24.5mm long, 9mm wide (incomplete, plates slightly disassociated). Cup conical, 3.7mm long, crushed. Radials 4 or 5, 3.7mm long, 3.2mm wide, subvertial longitudinally, gently convex transversely, proximal end weakly convex, distal end with peneplenary radial facets. Arms 10? Brachials cuneate, strongly convex transversely, with open V-shaped ambulacral groove.

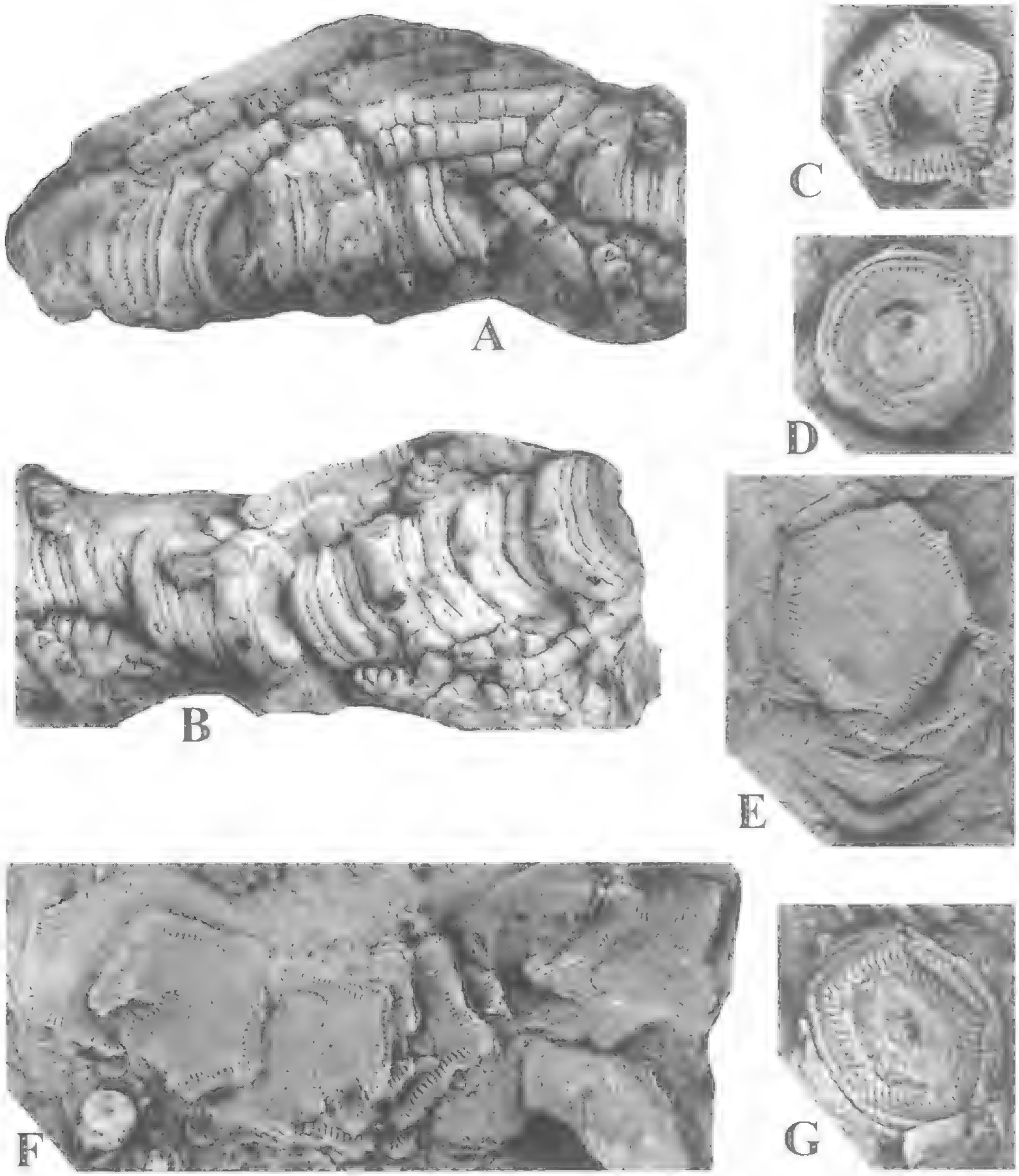


FIG. 33. *Nowracrinus ornatus* Willink, 1979. A,B, overlapping views of crushed pluricolumnal, QMF39018, ×2.8. C, facetal view of columnal QMF39077, ×4.2. D, facetal view of columnal QMF39021, ×4.2. E, facetal view of slightly disarticulated pluricolumnal QMF39016, ×3.3. F, facetal view of slightly disarticulated pluricolumnal QMF39017, ×3.4. G, facetal view of columnal QMF39076, ×4.4.

Cryptosyzygial and muscular articulation on alternating pairs of brachials distally. Pinnules stout. Stem pentagonal, 4mm attached to cup, 36mm unattached, heteromorphic; noditaxis N3231323. Columnals pentalobate, lobed to noded on petals, with strongly convex latus. Cirri close to cup, probably 5 per nodal. Cirrals short, round transversely, with convex latus.

REMARKS. This is the second specimen of *Tasmanocrinus* and probably represents a new

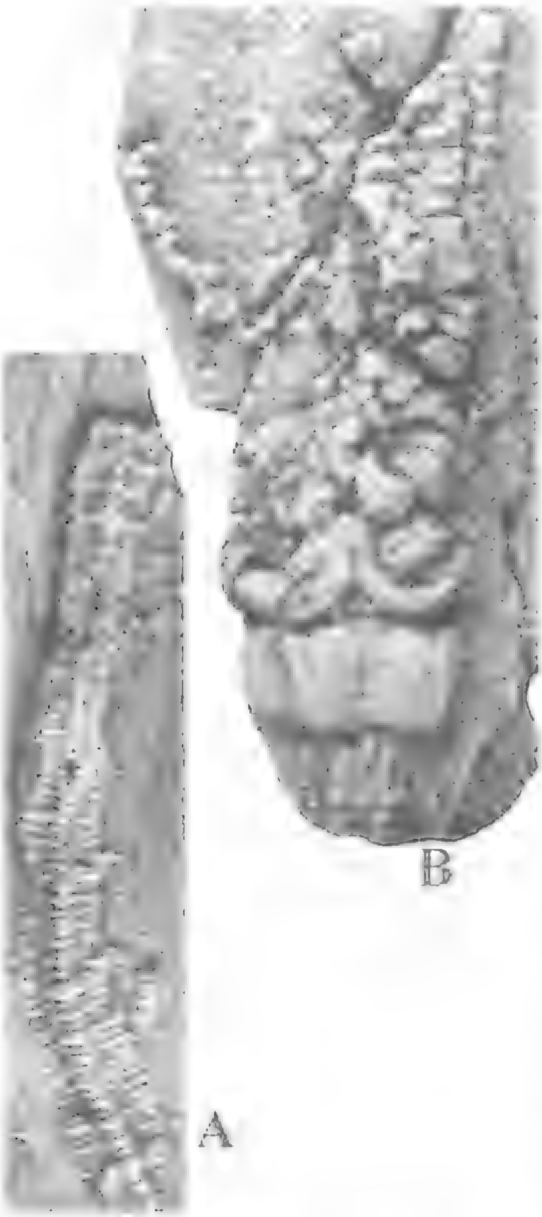



FIG. 34. A,B, *Tasmanocrinus* sp., lateral views of partial proximal stem and crown. Z3259. ×3.3.

species. It is crushed with plates slightly to moderately disassociated. Weathering and recrystallisation have destroyed facets on most exposed surfaces and ornamentation. A weak line of nodes or granules parallel to the intraradial sutures may be the remnant of coarser nodes similar to the aligned nodes on *T. mariensis* Willink, 1979. The elongate conical cup was possibly cryptodicyclic with the basals and infrabasals not visible in lateral view whereas the basal circlet formed a visible part of the cup of *T. mariensis*. In the radial circlet 3 plates are exposed and 2 are discernible through the thin layer of silt and clay covering the opposite side of the specimen. Willink (1979a) described *Tasmanocrinus* as having 3 radials bearing arms, a 4th radial lacking the distal end and a 5th plate as a radial-like anal. This specimen does not provide additional information concerning the uncertainty of the 4th radial. Only 2 of the 1st primibrachs are visible among the somewhat disarticulated arm plates.

Family affinities of *Tasmanocrinus* are uncertain. Cup shape has affinity with the Corythocrinidae. If there are only 3 arms it could be related to *Tribrachyocrinus*, but the arms are pinnulate not ramulate. The pentagonal stem, cirriferous close to the cup, is similar to some Ampelocrinidae. Brachial and columnal articulation show affinity with the Articulata and the peneplenary facets are unique within the Ampelocrinida.

## Order ISOCRINIDA Sieverts-Doreck, 1952
## Family ISOCRINIDAE Gislén, 1924

### **Archaeoisocrinus** gen. nov.

TYPE SPECIES. *Archaeoisocrinus occiduaustralis* from the middle Artinskian Cundlego Sandstone, Jimba Jimba Station, WA.

ETYMOLOGY. Greek *arche*, beginning, old, or primitive, and *Isocrinus*; refers to the beginning of the isocrinids.

DIAGNOSIS. Crown small, cylindrical, with arms enclosed. Cup discoidal, cryptodicyclic, infrabasals and basals in deep basal cavity, covered by proximal columnals; radials form base and cup wall; no anal or anal notch in cup. Radial facets plenary; wide gape between radials and 1st primibrach. Pentameral symmetry. Arms 10, branching isotomously on 2nd primibrach; brachials cuneate uniserial, with small dual internal entoneural canals, with 1 pinnule on long side of brachial above primibrachs. Brachial articulation alternating between oblique muscular and cryptosyzygial. Stem pentalobate; columnals thin, with strongly rounded convex latus.

REMARKS. *Archaeoisocrinus* differs from all other isocrinids, based on cups, in that the basals are within the basal cavity, and not visible in lateral view. *Archaeoisocrinus* is the oldest genus of the Isocrinidae, evolved from an ampelocrinid, possibly *Halogetocrinus*, in the Early Permian by

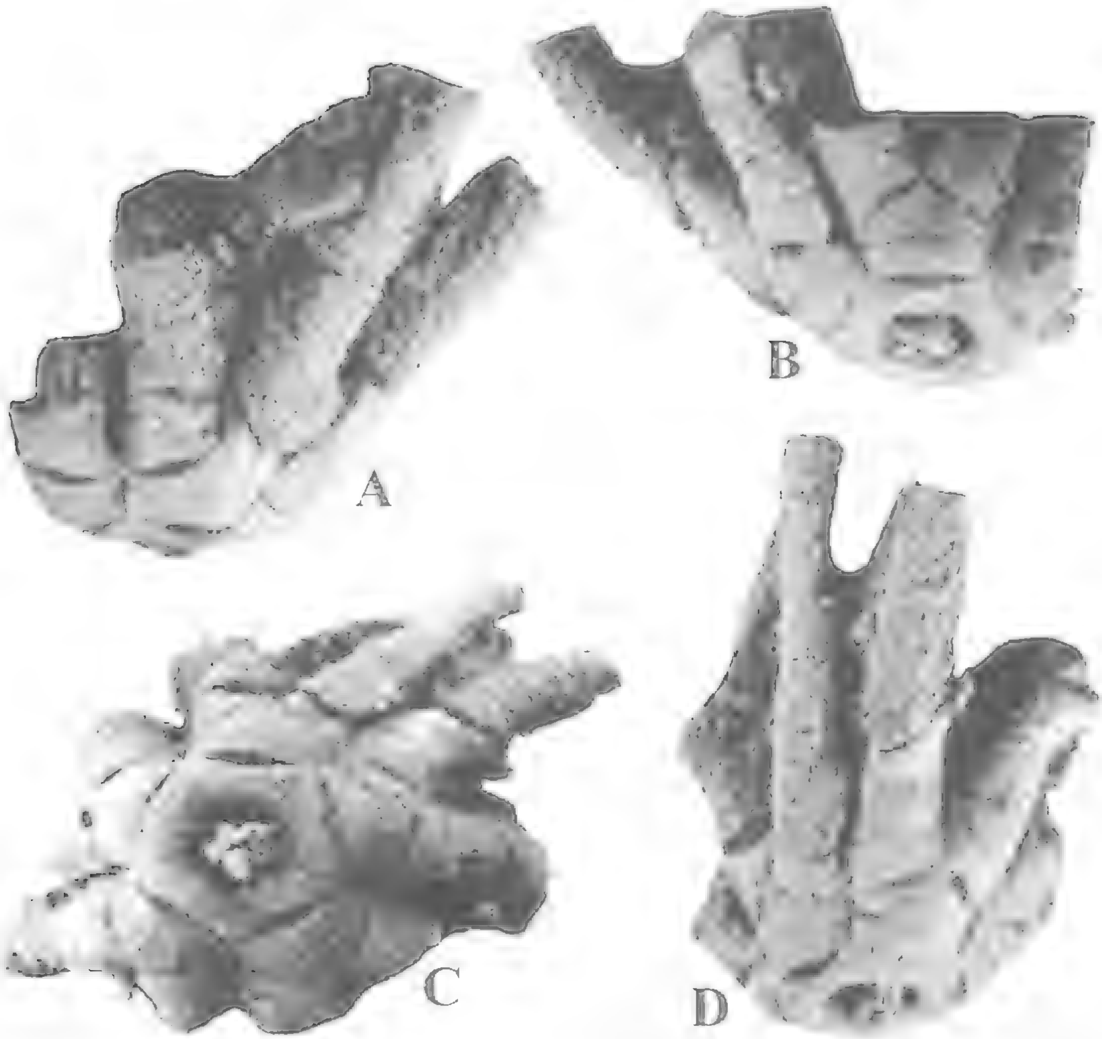



FIG. 35. A-D, *Archaeoisocrinus occiduaustralis* sp. nov. 3 lateral (A,B,D) basal (C) views of crown QMF38879, ×5.

removal of the anal plate from the cup and restriction of the basals to the basal invagination.

Previously, isocrinids were reported to range from Early Triassic to the Recent, with the Early Triassic specimens consisting of poorly preserved columnals lacking details of the articular facet (Rasmussen in Moore & Teichert, 1978). The middle Artinskian occurrence of *A. occiduaustralis* extends the range of the isocrinids back approximately 30 m.y.

**Archaeoisocrinus occiduaustralis** sp. nov.
(Figs 35, 36)

ETYMOLOGY. Latin *occidens*, western, and *australis*, southern.

MATERIAL. HOLOTYPE: QMF38879 from a nest of *Jimbacrinus bostocki* Teichert, 1954, from the Cundlego Sandstone on Jimba Jimba Station, WA. Slab found by Kevin Davy, Chris Johnston, and Tom Witherspoon and specimen found in preparation by Scott Vergiels. Crown retains the proximal 3 columnals, proximal part of all 10 arms, and medial parts of 2 arms.

DIAGNOSIS. As for genus.

DESCRIPTION. Crown small, cylindrical, with arms enclosed, 11.5mm long (incomplete), 9.6-16.7mm wide (13.1mm av. with arms partly opened). Cup discoidal, 0.8mm long, 4.2-4.5mm wide, with deep basal cavity, unornamented, with pentameral symmetry, without anal series in cup,

FIG. 36. *Archaeoisocrinus occiduaustralis* sp. nov., camera lucida drawing of distal facet of 9th secundibrach showing dual entoneural canals, QMF38879, ×20.

without anal notch on tip of indeterminate posterior radials, cryptodicyclic. Infrabasals? and basals within basal cavity, not visible in lateral or aboral views, covered by proximal columnals. Radials large, 1.4mm long (minimum), 2.6mm wide, strongly convex longitudinally, gently convex transversely, with proximal end in basal cavity, with medial part forming base of cup, distally gently upflared. Radial facet plenary, sloping down outward, 68° from horizontal, with large deep outer ligament pit, narrow outer marginal area. Large gape between radial and 1st primibrach. First primibrach 0.8mm long, 2.6mm wide on proximal end, 3.1mm wide on distal end, slightly convex longitudinally, moderately convex transversely. Axillary 2nd primibrach large, 1.3mm long, 3.2mm wide, slightly convex longitudinally, moderately convex transversely. All secundibrachs except 1st and 2nd moderately cuneate proximally, less cuneate distally, gently convex longitudinally, strongly convex transversely, nearly circular in transverse section, with single pinnule on long side; small dual entoneural canals circular in transverse section, centrally located; ambulacral groove small, V-shaped. First secundibrach rectilinear, 0.9mm long, 2.1mm wide. Second secundibrach small, nearly resorbed?, externally lens-shaped, restricted to middle of arms, 0.2mm long, 1mm wide. Third secundibrach cuneate, 1.6mm long on long side. 0.7mm long on short side, 2.1mm wide. Branching isotomous on 2nd primibrach in all rays, 10 arms, no distal branching on preserved arms. Straight muscular articulation between radials and primibrachs. Oblique muscular articulation between axillary 2nd primibrach and 1st secundibrach and between 3rd and 4th secundibrachs. Syzygial articulation between 1st and 2nd primibrachs and between 1st and 2nd, and 2nd and 3rd secundibrachs. Cryptosyzygial and muscular articulation on alternating pairs of brachials distally. Cryptosyzygial facet with faint culmina and crenellae on outer half of facet, radiating from entoneural canal. Stem pentalobate, facet not preserved. Columnals with strongly convex latus.

REMARKS. This delicate specimen is preserved with the arms slightly splayed around a sandstone matrix. The proximalmost columnals are distorted, masking the articular facet. Distal parts of the stem and arms are lacking.

## ACKNOWLEDGEMENTS

We sincerely appreciate the support of Don Mackenzie, Alex Cook and Bev Webster in field investigations that recovered many of the specimens described herein. Loan of specimens by the Queensland Geological Survey (through Sue Parfrey), Geological Survey of Western Australia, and Tasmanian Museum and Art Gallery are gratefully acknowledged. We are grateful to the managers of Williambury, Wandagee, Cherrabun, Carey Downs and Middalya Stations for access to collecting localities on their properties. Parks and Wildlife Service, granted access for collection of some Tasmanian specimens. Larry Davis provided some references. Paul Avern processed photographs. This project was supported by the National Geographic Society Grant 5982-97. GDW extends his appreciation to Washington State University for granting professional leave and to the Director of the Queensland Museum for use of facilites and office space during prosecution of this project. The reviews of Tom Baumiller and Gary Lane are kindly acknowledged.

## LITERATURE CITED

ANGELIN, N.P. 1878. Iconographia Crioideorum: in stratis Succiae Siluricis fossilium. (Samson & Wallin: Holmiae).

ARENDT, YU. A. 1981. Trekhrukie morskie lilii (Three armed crinoids). Trudy Palaeontological Institute, 189:1-195. (In Russian)

AUSICH, W.I. & BAUMILLER, T.K. 1993. Column regeneration in an Ordovician crinoid (Echinodermata): paleobiologic implications. Journal of Paleontology 67: 1068-1070.

BAMBACH, R.K. 1990. Late Palaeozoic provinciality in the marine realm. Geological Society Memoir 12: 307-323.

BATHER, F.A. 1893. The Crinoidea of Gotland: Pt. 1, The Crinoidea Inadunata. Kongliga Svenska Vetenskaps-Akademiens Handlingar 25(2): 1-201.

BAUMILLER, T.K. 1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. Palaeontology 33: 743-748.

1997. Crinoid functional morphology. In Waters, J. A. & Maples, C.G. (eds), Geobiology of Echinoderms. The Paleontological Society Papers 3: 45-68.

BRETT, C.E. 1978. Host-specific pit-forming epizoans on Silurian crinoids. Lethaia 11: 217-232.

1985. *Tremichnus*: a new ichnogenus of circular-parabolic pits in fossil echinoderms. Journal of Paleontology 59: 625-635.

BROADHEAD, T.W. 1981. Carboniferous camerate crinoid Subfamily Dichocrininae. Palaeontographica Abteilung A 176(4-6): 81-157.

DAY, R.W., WHITAKER, W.G., MURRAY, C.G., WILSON, I.H. & GRIMES, K.G. 1975. Queensland geology. Geological Survey of Queensland Publication 383: 1-194.

DICKINS, J.M., MALONE, E.J. & JENSEN, A.R. 1964. Subdivision and correlation of the Permian middle Bowen Beds, Queensland. Bureau of Mineral Resources Geology and Geophysics Report 70: 1-12.

DONOVAN, S. 1993. Contractile tissues in the cirri of ancient crinoids: criteria for recognition. Lethaia 26: 163-169.

ETHERIDGE, R. Jr 1892. A monograph of the Carboniferous and Permo-Carboniferous invertebrata of New South Wales. Part II. Echinodermata, Annelida, and Crustacea. Memoirs of the Geological Survey of New South Wales, Palaeontology 5: 65-131, pls 12-22.

1915. Western Australian Carboniferous fossils, chiefly from Mount Marmion, Lennard River, West Kimberley. Western Australia Geological Survey, Bulletin 58: 7-49.

GLENISTER, B.F., ROGERS, F.S. & SKWARKO, S.K. 1993. Ammonoids. Geological Survey of Western Australia Bulletin 136: 54-63.

KAMMER, T. & AUSICH, W.I. 1993. Advanced cladid crinoids from the Middle Mississippian of the east-central United States: intermediate-grade calyces. Journal of Paleontology 67: 614-639.

LANE, N.G. & WEBSTER, G.D., 1966. New Permian crinoid fauna from southern Nevada. University of California Publications in Geological Sciences 63: 1-60.

LYON, S.S. & CASSEDAY, S.A. 1860. Description of nine new species of Crinoidea from the sub-Carboniferous rocks of Indiana and Kentucky. American Journal of Science and Arts, series 2, 29: 68-79.

MAREZ OYENS, F.A.H.W. De 1940. Neue Permische Krinoiden von Timor. Geological Expedition Lesser Sunda Island 1: 285-348.

MILLER, J. S. 1821. A natural history of the Crinoidea, or lily-shaped animals; with observations on the genera, *Asteria*, *Euryale*, *Comatula* and *Marsupites*. (Bryon & Co.: Bristol).

MOORE, R.C. & JEFFORDS, R.M. 1968. Classification and nomenclature of fossil crinoids based on studies of dissociated parts of their columns. The University of Kansas Paleontological Contributions, Echinodermata Article 9: 1-86, 28 pls.

MOORE, R.C. & PLUMMER, F.B. 1940. Crinoids from the Upper Carboniferous and Permian strata in Texas. University of Texas Publication 3945: 1-468.

MOORE, R.C. & TEICHERT, C. (eds) 1978. Treatise on invertebrate paleontology. Part T. Echinodermata 2. 3 vols. (Geological Society of America & University of Kansas: Lawrence, Kansas).

PABIAN, R.K., BOARDMAN, D.R., II & HOLTERHOFF, P.F. 1989. Paleoecology of Late Pennsylvanian and Early Permian crinoids from north-central Texas. Texas Tech University Studies in Geology 2: 291-303.

PABIAN, R.K. & STRIMPLE, H.L. 1993. Taxonomy, paleoecology and biostratigraphy of the crinoids of the South Bend Limestone (Late Pennsylvanian-Missourian, ?Virgilian) in southeastern Nebraska and southeastern Kansas. Conservation and Survey Division, University of Nebraska-Lincoln, Professional Paper 1: 1-55.

REED, F.R.C. 1928. A Permo-Carboniferous marine fauna from the Umaria Coal-field. Records Geological Survey India 60: 367-398, pls 31-34.

1933. Notes on some lower Palaeozoic fossils from the southern Shan States. Records Geological Survey of India 66: 188-211.

SHI, G.R. & McLOUGHLIN, S. 1997. Permian stratigraphy, sedimentology and palaeontology of the southern Sydney Basin, eastern Australia. School of Aquatic Science and Natural Resources Management, Deakin University Technical Paper 1997/2: 1-59.

SIEVERTS-DORECK, H. 1942. Crinoioden aus dem Perm Tasmaniens. Zentralblatt für Mineralogie, Geologie und Paläontologie, Monatschefte 3: 80-87.

SIMMS, M.J. 1988. The phylogeny of post-Palaeozoic crinoids. Pp. 269-284. In Paul, C.R.C. & Smith, A.B. (eds), Echinoderm phylogeny and evolutionary biology. (Clarendon Press: Oxford).

SIMMS, M.J. & SEVASTOPULO, G.D. 1993. The origin of articulate crinoids. Palaeontology 36: 91-109.

SIMPSON, G.G. 1961. Principles of animal taxonomy. (Columbia University Press:New York).

STRIMPLE, H.L. 1971. A Permian crinoid from Coahuila, Mexico. Journal of Paleontology 45: 1040-1042.

STRIMPLE, H.L. & FREST, T. 1979. Points of generation and partial regeneration of the column of *Euonychocrinus simplex* (Crinoidea: Flexibilia). Journal of Paleontology 53: 216-220.

STRIMPLE, H.L. & MOORE, R.C. 1971. Crinoids of the Francis Shale (Missourian) of Oklahoma. University of Kansas Paleontological Contributions Paper 55: 1-20.

STRIMPLE, H.L. & WATKINS, W.T. 1969. Carboniferous crinoids of Texas with stratigraphic implications. Palaeontographica Americana 6(40): 139-275, pl. 30-56.

TEICHERT, K. 1949. Permian crinoid *Calceolispongia*. Memoir of the Geological Society of America 34: 1-132.

1954. A new Permian crinoid from Western Australia. Journal of Paleontology 28: 70-75.

VAN SANT, J. 1964. Crawfordsville (Indiana) crinoid studies. University of Kansas Paleontological Contributions, Echinodermata Article 7: 1-136.

WANNER, J. 1916. Die permischen Echinoderm von Timor, I Teil. Paläontologie von Timor 6: 1-329, pls. 94-115.

1924. Die permischen Echinoderm von Timor, II Teil. Jaarboek van het Mijnwezen in Nederlandsch Oost-Indië 5. 1921, 3: 1-328, 22 pls.

1937. Neue Beiträge zue Kenntnis der permischen Echinodermen von Timor, VIII-XIII. Palaeontographica, Supplement 4(2): 59-212.

WEBSTER, G.D. 1974. Crinoid pluricolumnal noditaxis patterns. Journal of Paleontology 48: 1283-1288.

1987. Permian crinoids from the type-section of the Callytharra Formation, Callytharra Springs, Western Australia. Alcheringa 11: 95-135.

1990. New Permian crinoids from Australia. Palaeontology 33: 49-74.

1997. Lower Carboniferous echinoderms from northern Utah and western Wyoming. Paleontology Series, v. 1, Utah Geological Survey Bulletin 128: 1-65.

WEBSTER, G.D. & HOUCK, K.J. 1998. Middle Pennsylvanian, late Atokan-early Desmoinesian, echinoderms from an intermontane basin, the Central Colorado Trough. Journal of Paleontology.72: 1054-1072.

WEBSTER, G.D. & JELL, P.A. 1992. Permian echinoderms from Western Australia. Memoirs of the Queensland Museum 32: 311-373.

WEBSTER, G.D., JELL, P.A. & DEREWETZKY, A.N. in press. Palaeobiogeography of Permian echinoderms of Australia. Permian of Eastern Tethys Symposium Volume.

WEBSTER, G.D., & LANE, N.G. 1967. Additional Permian crinoids from southern Nevada. University of Kansas Paleontological Contributions, Paper 27: 1-32.

1970. Carboniferous echinoderms from the southwestern United States. Journal of Paleontology 44: 276-296, pls 55-58.

WELLER, S. 1909. Description of a Permian crinoid fauna from Texas. Journal of Geology 17: 623-635.

WILLINK, R. 1978. Catillocrinids from the Permian of eastern Australia. Alcheringa 2: 83-102.

1979a. Some conservative and highly-evolved Permian crinoids from eastern Australia. Alcheringa 3: 117-134.

1979b. The crinoid genera *Tribrachyocrinus* M'Coy, *Calceolispongia* Etheridge, *Jimbacrinus* Teichert and *Meganotocrinus* n. gen. in the Permian of eastern Australia. Palaeontographica Abteilungen A 165: 137-194.

1980a. A new coiled-stemmed camerate crinoid from the Permian of eastern Australia. Journal of Paleontology 54: 15-34.

1980b. Two new camerate crinoid species from the Permian of eastern Australia. Alcheringa 4: 227-232.

WRIGHT, J. 1937. Scottish Carboniferous crinoids. Geological Magazine 74: 385-411, pls 13-16.

1951. The British Carboniferous Crinoidea. Palaeontographical Society Monograph, 1(4): 103-148, pls 32-40.

YAKOVLEV, N.N. 1933. Dve verkhnepermskhe morskie lilii iz zakavkaziya [Two Upper Permian crinoids from the Transcaucasus]. Izvestiya Akademii Nauk SSSR, Leningrad 7: 975-879. (In Russian)

1956. Organism i sreda. Stati po paleoeckologii besnozvonochnykh 1913-1956. [Organisms and surroundings. Writings on paleoecology of invertebrates, 1913-1956]. Akademii Nauk SSSR. 139p. (In Russian)

## APPENDIX 1

Queensland Museum localities referred to in text.

QML518 - Late Artinskian Condamine Beds, S side Lucky Valley Creek, Elbow Valley area, SW of Warwick, SE Qld. Magellan GPS coordinates 28°22'31"S, 152°08'19"E.

QML757 - Late Sakmarian or early Artinskian Callytharra Formation, N side of bladed track from Callytharra Homestead to Byro Homestead in W most exposures 1.5km W of type section S of Wooramel River, WA. 25°52'30"S, 115°29'E. Wooramel Sheet SG50-5, 1966.

QML758 - Late Sakmarian or early Artinskian Callytharra Formation, N side of bladed track from Callytharra Homestead to Byro Homestead as track enters dry wash tributary to Wooramel River, lowermost fossiliferous shale and marl capped by limestone in lower fossiliferous unit. Type section of Callytharra Formation. 25°52'30"S, 115°30'05"E, Glenburgh Sheet SG50-6, 1963.

QML759 - Late Sakmarian or early Artinskian Callytharra Formation, second fossiliferous shale and marl capped by limestone in type section of Callytharra Formation. South side of track and stratigraphically higher than QML758.

QML772 - Wuchiapingian Cherrabun Member of Hardman Formation; bench in lower slope below cliff 0.5-1.0km NNW of type section, Millyit Range; GR767877 Crossland Sheet SE51-16, 1977, WA. Magellan GPS coordinates 19°10'45"S, 125°32'35"E.

QML806 - Late Permian, Flat Top Formation, Back Creek Group; halfway up small rise, 1.3 km E on Uncle Tom road from Leichardt Highway, S of Banana, Queensland. Coll. A. Cook & M. Wade.

QML859 - Wandrawandian Siltstone; Point Upright, wavecut platform below lighthouse, Uladulla, NSW.

QML1141 - Middle Artinskian Bulgadoo Shale, upper part of type section SE of Donnelly's Well, Williambury Stn, WA. Magellan GPS coordinates 24°05'45"S, 115°05'40"E.

QML1145 - same as QML772.

QML1146 - Wuchiapingian Cherrabun Member of Hardman formation; bench in lower slope below cliff, Millyit Range, WA. Magellan GPS coordinates 19°10'28"S, 125°32'26"E.

QML1217 - Late Artinskian, basal massive sandstone of the Wandagee Sandstone, exposed in type section along the Minilya River, Wandagee Station, WA. Magellan GPS coordinates 23°44'20"S, 114°25'02"E.

QML1232 - Early Artinskian, upper part of Callytharra Formation, E limb of Gooch Range, W side of valley, E facing slope, S of Minilya-Lyndon road, up small drainage just S of where bladed road turns E to cross valley, WA. Magellan GPS coordinates 23°54'22"S, 114°56'54"E.

QML1233 - Float in limestone below QML1232.

QML1237 - Early Artinskian, upper part of Callytharra Formation, lower crinoidal rich zone, N side of Minilya-Lyndon Road, flat below slope, 50m SE of ridge, E limb of Gooch Range, WA. Magellan GPS coordinates 23°53'48"S, 114°56'48"E.

QML1240 - Early Artinskian, upper part of the Callytharra Formation, top of first bench nearest road, N side of Minilya-Lyndon road, E limb of Gooch Range, WA. Magellan GPS coordinates 23°53'41"S, 114°56'35"E.

QML1247 - Kansas Beds, Early Permian, Artinskian; roadcut and quarry on W side of cut at top of first hill on Blackwells Road, 0.8km W of junction with Highway A10. Blackwells Road is 14km S of junction A10 and B26, Yolla, Tasmania. Coordinates 83.25 35.80 Burnie Sk55-3, 1973.

GSWAL119377 - Artinskian, Billidee Formation, 4th limestone, Australian Map Grid coordinates Zone 50, 326340E, 7296860N, S of Mt Sandiman sheds. Coll. A.J. Mory.

## APPENDIX 2

List of described Permian crinoid taxa from stratigraphic units of Western Australia, Queensland, New South Wales and Tasmania.

Cherrabun Member, Hardman Formation, Wuchiapingian, WA.
- *Neocamptocrinus millyitensis* Webster & Jell, 1992
- *Metacalceolispongia cherrabunensis* (Webster & Jell, 1992)

Wandagee Sandstone, late Artinskian, WA.
- *Calceolispongia abundans* Teichert, 1949

Cundlego Sandstone, middle Artinskian, WA.
- *Archaeoisocrinus occiduaustralis* gen. et sp. nov.

Billidee Formation, early Artinskian, WA.
- *Dichocrinus*? sp.

Callytharra Formation, late Sakmarian to early Artinskian, WA.
- *Neocamptocrinus*? sp.
- *Glaukosocrinus middalyaensis* sp. nov.
- *Parabursacrinus granulatus* Wanner, 1949
- Timorechinid gen. indet.
- Poteriocrinitid indet., arms 1
- Poteriocrinitid indet., arms 2
- Poteriocrinitid indet., arms 3
- *Loxocrinus booni* Marez Oyens, 1940
- *Loxocrinus* sp. 1
- *Loxocrinus* sp. 2
- *Prophyllocrinus* sp. 1
- *Prophyllocrinus* sp. 2
- *Prophyllocrinus* sp. 3
- Sagenocrinit id indet.

Flat Top Formation, Wordian, Qld.
- *Auliskocrinus*? *bananaensis* sp. nov.
- *Tribrachyocrinus*? sp., arm fragment

Condamine Beds, latest Artinskian or early Roadian, Qld.
- *Neocamptocrinus* sp. nov.
- *Platycrinites halos* sp. nov.
- Platycrinitid indet., columnals
- *Necopinocrinus tycherus* gen. et sp. nov.
- *Eidosocrinus condaminensis* gen. et sp. nov.
- *Pedinocrinus*? *nodosus* sp. nov.
- Stellarocrinid? gen. et sp. nov.
- *Spaniocrinus geniculatus* sp. nov.
- *Sundacrinus medius* sp. nov.
- *Moapacrinus cuneatus* sp. nov.
- *Eoindocrinus praecontignatus* Arendt, 1981
- *Calceolispongia* sp.
- Poteriocrinitid indet., arm fragment 1
- Poteriocrinitid indet., arm fragment 2
- Poteriocrinitid indet., arm fragment 3

Catherine Sandstone, late Artinskian, Qld.
- *Neocamptocrinus catherinensis* sp. nov.

Unknown stratigraphic unit, late Artinskian or early Roadian, Qld.?
- *Meganotocrinus princeps* (Etheridge, 1892)

Berridale Limestone, early Artinskian, Tas.
- *Calceolispongia gerthi* Willink, 1979

Kansas Beds, early Artinskian, Tas.
- Order indet., basal and radial plates
- *Nowracrinus ornatus* (Etheridge, 1892)

Malbina Formation, late Artinskian, Tas.
- *Tribrachyocrinus corrugatus* Ratte, 1885
- *Tribrachyocrinus granulatus* Etheridge, 1892
- *Tasmanocrinus* sp.

Wandrawandian Siltstone, late Artinskian, NSW.
- *Anaglyptocrinus willinki* gen. et sp. nov.

**A MONASTERID STARFISH FROM THE PERMIAN OF TIMOR.** *Memoirs of the Queensland Museum 43(1): 340. 1999:–* Among a large collection of Permian fossils made by Brad Macurda from the Indonesian island of Timor and deposited in the Museum of Paleontology at the University of Michigan is a fragment (2 arms) of a small starfish, the first record of the group from that island which has yielded the world's most diverse Permian echinoderm fauna. The locality label reads 'No. 51702, 1 specimen, Permian, Tonino I, Timor'. This locality refers almost certainly to the known Permian locality Tonino (=Toeninoe of Macurda, 1983) Noil (=stream) 1-2km SE of Basleo, SE Timor.

Order PUSTULOSIDA Spencer, 1931

Suborder MONOMARGINALINA Kesling, 1969

Family MONASTERIDAE Schuchert, 1915

**Genus** nov.

(Fig. 1)

DESCRIPTION. Arms 8mm long, 4mm wide proximally and 2mm deep, upturned strongly at distal tip. Dorsally all plates strongly convex to bulbous; median column of radials or carinals of 4 plates, with distal one greatly inflated and terminating arm; inferomarginal columns enclosing arms laterally and visible in both dorsal and ventral views, each column of 3 convex plates; with 3 interradial plates not inflated, with small axil visible dorsally and ventrally. Ventral surface mainly 2 columns of large adambulacrals; adambulacrals short and wide, becoming narrower distally, transversely convex, in contact along axis so concealing ambulacrals. Mouth frame disarticulated, unclear.

REMARKS. Following Kesling's (1969) review, this specimen fits the concept of the Monasteridae because it has short wide adambulacrals ventrally and dorsally the column of strong dorsal carinals contiguous with the inferomarginals that enclose the arms laterally. The family is known from Australia (Kesling, 1969) and South West Africa (Lane & Frakes, 1970) but all known Australian species are represented by specimens very much larger (at least 5 times) than this Timorese specimen so its morphology is probably that of a juvenile. It is, therefore, difficult to make meaningful comparisons with confidence and makes any formal taxonomic decisions inadvisable. The most distinctive feature of the new specimen is the extremely large terminal radial plate which is highly suggestive of a new genus. It is difficult to imagine such a distinctive feature disappearing with growth and none of the known species of the family have such an arm termination. However, with only 2 arms of a juvenile and no disc details available I find myself in the same position as Lane & Frakes (1970), unable to name a new taxon based on it. The occurrence of monasterids in Timor further strengthens the faunal similarities between that island and Western Australia so evident among crinoids and blastoids (Webster & Jell, 1992).

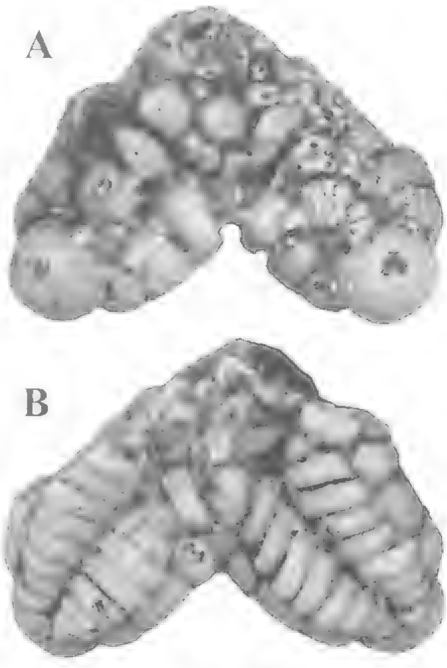



FIG. 1. Monasteridae gen. nov. UMMP51702, ×7.5. A, dorsal view. B, ventral view.


### Literature cited

KESLING, R.V. 1969. Three Permian starfish from Western Australia and their bearing on revision of the Asteroidea. Contributions from the Museum of Paleontology, at the University of Michigan 22: 361-376

LANE, N.G. & FRAKES, L.A. 1970. A Permian starfish from South West Africa. Journal of Paleontology 44: 1135-1136

MACURDA, D.B. 1983. Systematics of the fissiculate Blastoidea. Papers in Paleontology from the Museum of Paleontology at the University of Michigan 22: 1-291

WEBSTER, G.D. & JELL, P.A. 1992. Permian echinoderms from Western Australia. Memoirs of the Queensland Museum 32: 311-373


*Peter A. Jell, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia; 17 May 1999.*

# A NEW CORNUTE CARPOID FROM THE UPPER CAMBRIAN (IDAMEAN) OF QUEENSLAND

ANDREW B. SMITH AND PETER A. JELL

Smith, A.B. & Jell, P.A. 1999 06 30: A new cornute carpoid from the Upper Cambrian (Idamean) of Queensland. *Memoirs of the Queensland Museum* **43**(1): 341-350. Brisbane. ISSN 0079-8835.

The first Cambrian carpoid from Australia, *Drepanocarpos australis* gen. et sp. nov. is described from the Chatsworth Limestone in the Lily Creek section at Chatsworth 100km north of Boulia, western Queensland. Its age is the *Peichiashania secunda - Prochuangia glabella* Zone, latest Idamean Stage (=mid Franconian Stage), in the medial Late Cambrian. It belongs to the cornute Family Phyllocystidae, having cothurnopores, rigidly plated dorsal surface and flexible plated ventral surface, a well-defined marginal frame with ventral vertical strut and dorsal transverse strut and 6 well-defined rings in the proximal part of tail. ❒ *Carpoid, Phyllocystidae, Upper Cambrian, Queensland.*

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Carpoids are rare in Upper Cambrian rocks. Ubaghs (1963) described one from a unique specimen and two others from fragmentary material of uncertain generic placement; all 3 came from a single locality and horizon in the early Trempeleauan Whipple Cave Formation in Nevada. Sumrall et al. (1997) featured 6 carpoids from the Upper Cambrian of Wyoming and Nevada with none of them represented by a complete specimen and all known from 1 or 2 specimens or a single slab; the 3 cornutes are assigned specific names in 2 new genera, *Acuticarpus* and *Archaeocothurnus*, the other 3 taxa are left in open nomenclature. Ubaghs (1999) described a new genus, *Lobocarpus*, from the Upper Cambrian of Montagne Noire, southern France. Known Australian carpoids are reported elsewhere in this Memoir (Ruta & Jell, 1999a-e) and derive from the latest Ordovician to Early Devonian clastic sequences of Victoria and Tasmania. However, the Cambrian and great majority of the Ordovician in Australia have yielded no carpoids, and cornutes have never been recorded from Australia.

At Museum of Victoria Locality NMVPL1597 (= Bureau of Mineral Resources Locality K204 of Shergold, 1982) in a 4m thick grey micaceous limestone forming a bench on the low limestone rise 3.5km S of Chatsworth Homestead 60km SW of Duchess, W Queensland is a rich silicified fauna of trilobites (*Connagnostus* sp. undet., *Iveria iverensis, Lorretina depressa, Peichiashania secunda, Prochuangia glabella, Pseudagnostus parvus, Pseudagnostus* sp. undet.), gastropods, monoplacophorans, brachiopods, hyoliths, sponges and echinoderms. The last mentioned group was partly described by Jell et al. (1985) who treated the 'eocrinoid' *Riddersia watsonae* and noted an isorophid edrioasteroid and by Smith & Jell (1990) who described the isorophids *Hadrodiscus parma* and *Chatsworthia spinosa* (=isorophid of Jell et al. 1985) and the edrioblastoid *Cambroblastus enubilatus*. Details of the location are available in Shergold (1982, figs 3,4) who also dated the bed, based on trilobites, as within his *Peichiashania secunda - Prochuangia glabella* Zone, the youngest within the Idamean Stage.

The fossils are coarse silica replacements of extremely fine structures and in no specimen is replacement complete. Unravelling the structure of the species has been achieved by gathering some information from each of 12 available specimens and piecing it together into a picture of the whole animal. This approach necessitates more illustrations and camera lucida drawings than is normal to understand the species.

Illustrated material is deposited in the Queensland Museum, Brisbane (QMF) and the Natural History Museum, London (BMNH). Plate lettering, orientation and terminology follow Jeffries et al. (1987) without necessarily entering the debate on the affinities and possible biology of carpoids.

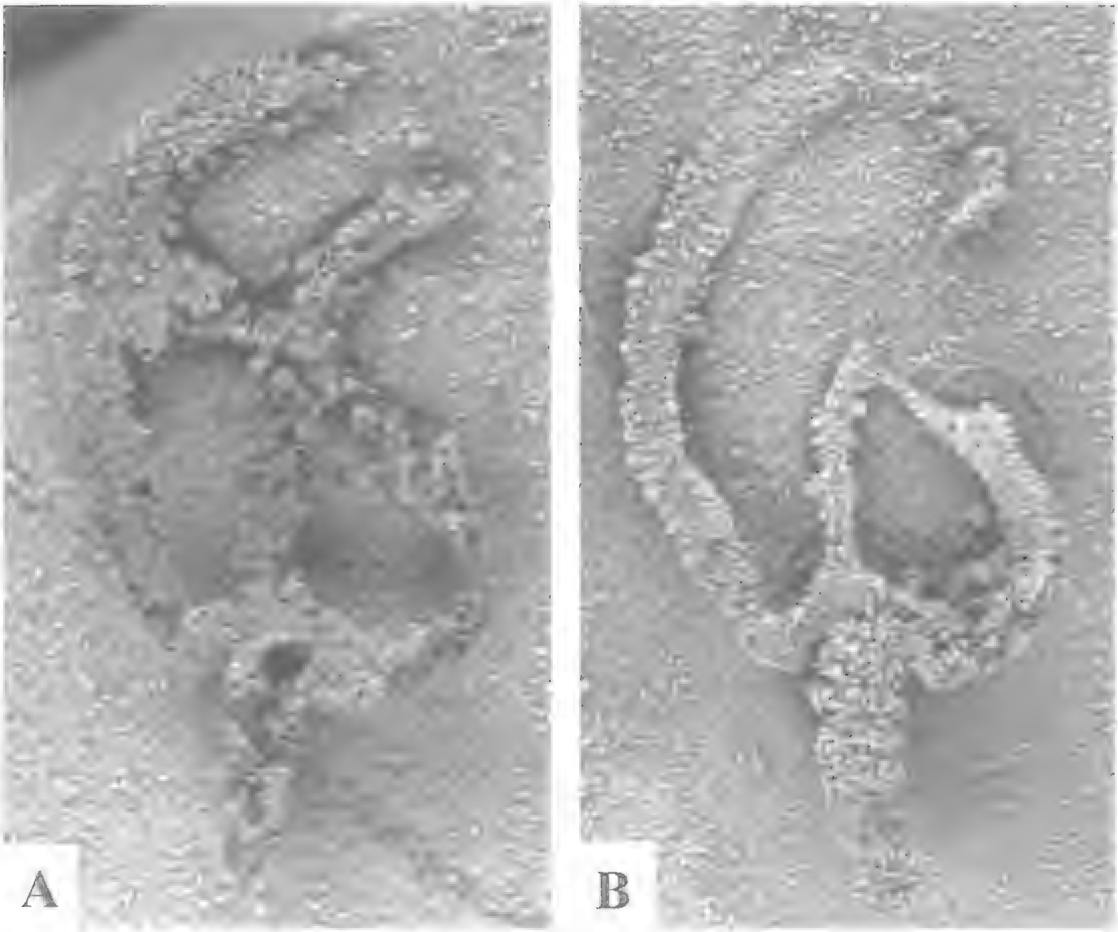


FIG. 1. *Drepanocarpos australis* gen. et sp. nov., ventral surface uppermost, ×9. A, QMF17862. B, QMF17860.

## SYSTEMATIC PALAEONTOLOGY

### Order CORNUTA Jaekel, 1901
### Family ?PHYLLOCYSTIDAE Derstler, 1979
### **Drepanocarpos** gen. nov.

TYPE SPECIES. *Drepanocarpos australis* sp. nov.

ETYMOLOGY. Greek *drepanon*, a sickle or blade, alluding to the curved marginal frame, and *carpos*, a fruit - the common name applied to this group.

RANGE AND DISTRIBUTION. Upper Cambrian (Idamean = Franconian) of Queensland.

DIAGNOSIS. Cornute with body longer than wide, with strong marginal frame and ventral strut; ventral surface composed of a few large plates; dorsal tegmen of many small platelets. Gill slits 4-5, as cothurnopores in the posterior left-hand side in an embayment of marginal plate k, framed by skeletal elements. A transverse bar on the dorsal surface separates the body into proximal and distal portions. Proximal part of appendage with 6 well-defined rings, distal part narrower. No strongly differentiated stylocone.

REMARKS. This genus belongs to the Cornuta on account of its marginal frame and distinctive bipartite appendage. Of the 3 families currently recognised, Scotiaecystidae has a very distinctive gill slit morphology quite different from that in *Drepanocarpus* and thus need not be considered further.

The elongate body form, tesselated dorsal plating and finer platelets of the ventral surface are typical of phyllocystids such as *Lobocarpus* Ubaghs, 1999, the only named phyllocystid

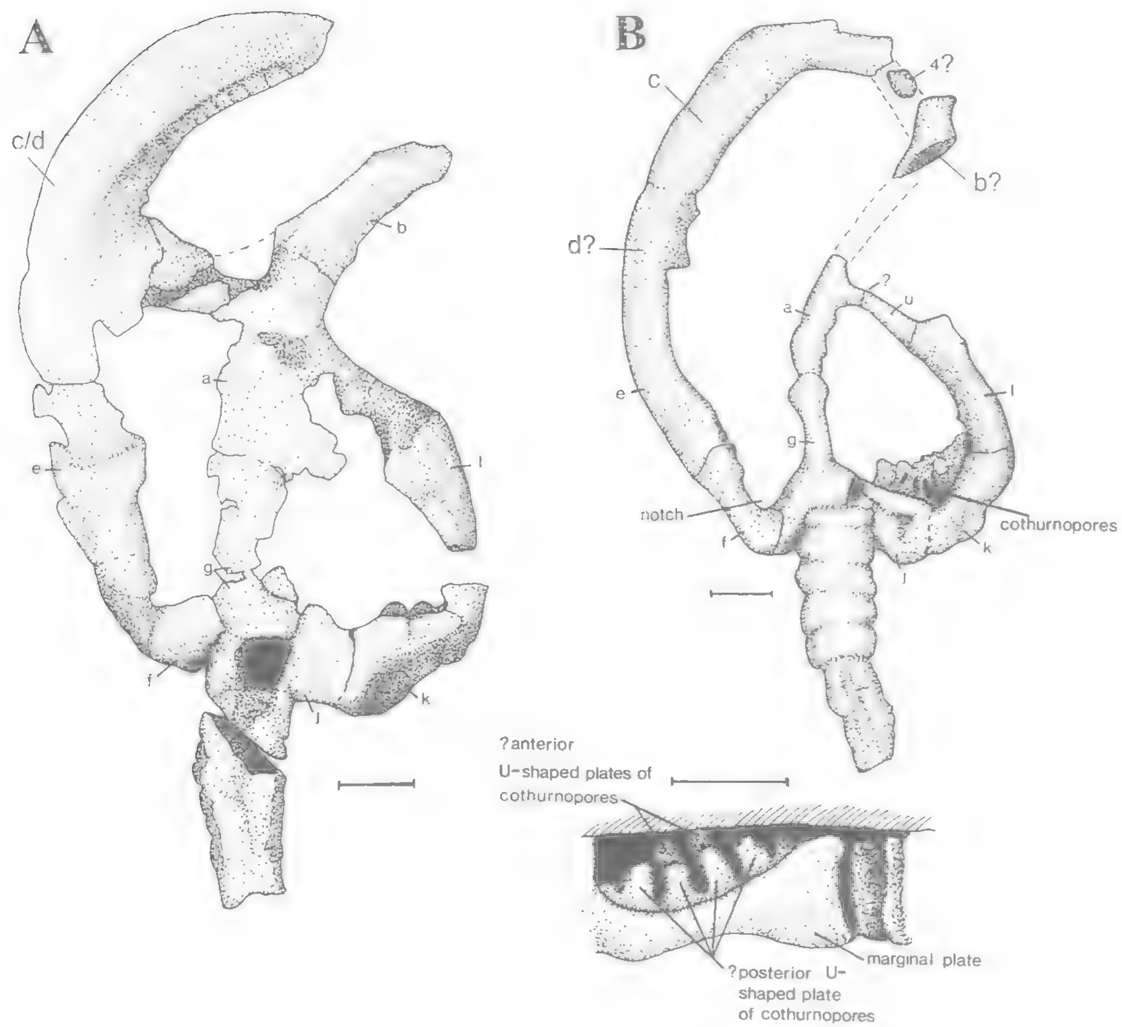


FIG. 2. *Drepanocarpos australis* gen. et sp. nov., camera lucida drawings of ventral surface with plating interpretation (plate lettering follows the system of Jefferies et al., 1987). A, QMF17862. B, QMF17860. C, posterior view of the left hand side of QMF17860, dorsal surface uppermost. Cross hatching = sediment. Scale bar = 1mm.

known from the Cambrian. Note that Ubaghs was equivocal in his family assignment.

*Lobocarpus* differs from *Drepanocarpos* in having a much more heart-shaped body, with broad, flange-like marginals and a less well-developed central strut. *Drepanocarpos* differs from the type species of *Phyllocystis* in having a more asymmetric body, deeper left marginal indentation and in having larger and fewer dorsal plates.

With the uncertainty of classification among the early Palaeozoic cornutes some comparisons with ceratocystid and cothurnocystid Cambrian forms are warranted.

*Drepanocarpos* resembles Middle Cambrian *Ceratocystis* Jaekel, 1901 from Europe in its overall shape, although the body is more rounded proximally. The ventral surface is composed of a small number of large sutured plates, these probably being extensions of the marginal plates.

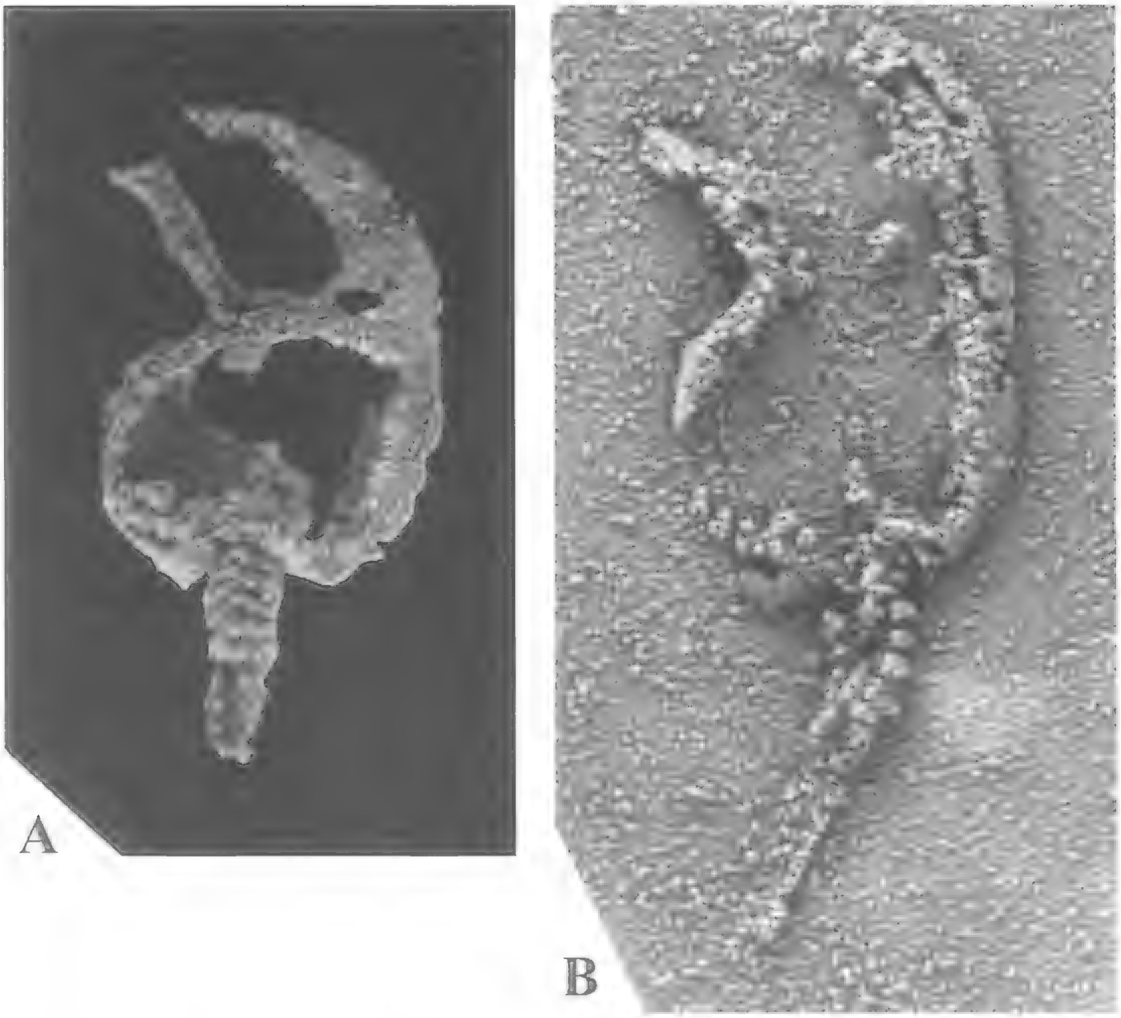

FIG. 3. *Drepanocarpos australis* gen. et sp. nov., dorsal surface uppermost, ×9. A, QMF17861. B, BMNH EE6344.

*Drepanocarpos* differs from *Ceratocystis*, however, in a number of important details. Most importantly its gill slits are not in the form of sutural pores but rather cothurnopores.

*Protocystites meneviensis* from the Middle Cambrian of Wales (Jefferies *et al*., 1987) closely resembles *Ceratocystis* in shape but has reduced ventral plating and a better defined proximal tail, like *Drepanocarpos*. It differs from *Drepanocarpos* in the absence of a sagittal strut on the interior of plates a and g and the very different shape and arrangement of the distal spines and gill slits, which resemble those of *Ceratocystis*.

'*Phyllocystis* sp.' and *Nevadaecystis americana* Ubaghs from the latest Cambrian of Nevada (Ubaghs, 1963), *Cothurnocystis* ? *bifida* Ubaghs & Robison from the Middle Cambrian of Utah (Ubaghs & Robison, 1988) and an unnamed cothurnocystid from the Middle Cambrian Spence Shale of Utah, U.S.A. (Sprinkle, 1976) have cothurnopores (oval spout-like openings within the dorsal tegmen) and well-defined rings in the proximal part of the tail. *Cothurnocystis* ? *bifida* is more L-shaped in outline than *Drepanocarpos* and plate l forms the distal left-hand angle of the head carrying a very large process. It also has a ventral tegmen of retiform

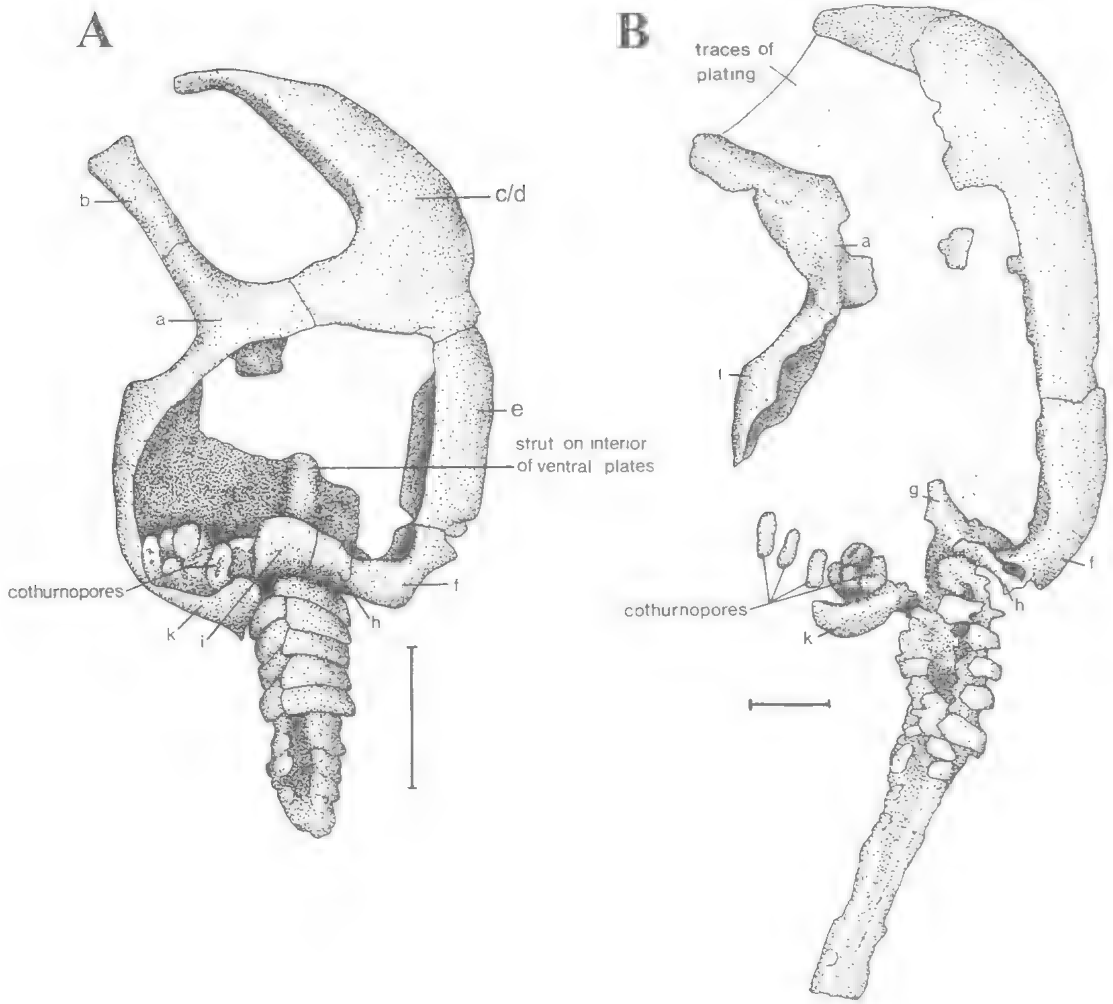


FIG. 4. *Drepanocarpos australis* gen. et sp. nov., camera lucida drawings of dorsal surface with plating interpretation (plate lettering follows the system of Jefferies et al., 1987). A, QMF17861. B, BMNH EE7344. Scale bar = 1mm.

stereom, possibly in the form of a continuous sheet of calcified integument. Unlike *Drepanocarpos* plates a and c are not united by a transverse bar, although this may be a result of poor preservation.

*Nevadaecystis* is laterally elongate and shaped like *Cothurnocystis*, with similar highly developed lateral blade-like processes on plate l. Also, like *Cothurnocystis* but unlike *Drepanocarpos*, plates a and c in *Nevadaecystis* are unconnected and the distal border of the buccal cavity lacks plate 4. Like *Drepanocarpos* it has a ventral surface of large plates, extensions of the marginals, and a dorsal tegmen of much smaller platelets. There is also a saggital strut formed presumably from the internal thickening of two of these plates. Jefferies et al. (1987, fig. 12) interpreted *Nevadaecystis* as having an additional plate x, like *Cothurnocystis fellensis*. However, in the reconstruction of Ubaghs & Robison (1988, fig. 11.1) no such plate is shown.

The unnamed cornute from the Middle Cambrian Spence Shale in Utah (Sprinkle, 1976) resembles *Drepanocarpos* in shape and plating arrangement, in lacking obvious appendages to the marginal frame, in having a dorsal tegmen of small platelets, in having a smoothly rounded right margin and in having cothurnopores across

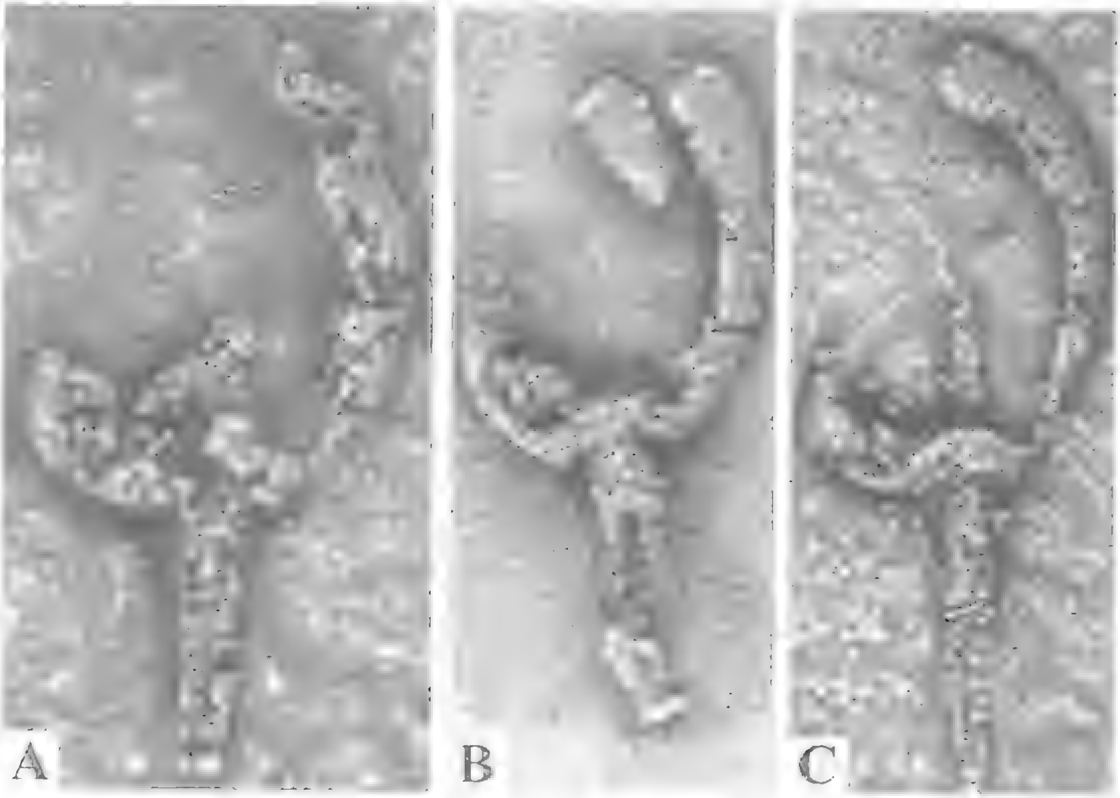


FIG. 5. *Drepanocarpos australis* gen. et sp. nov., dorsal views showing cothurnopores. A, QMF17866, ×11. B, QMF17863, ×8. C, BMNH EE6345, ×8.

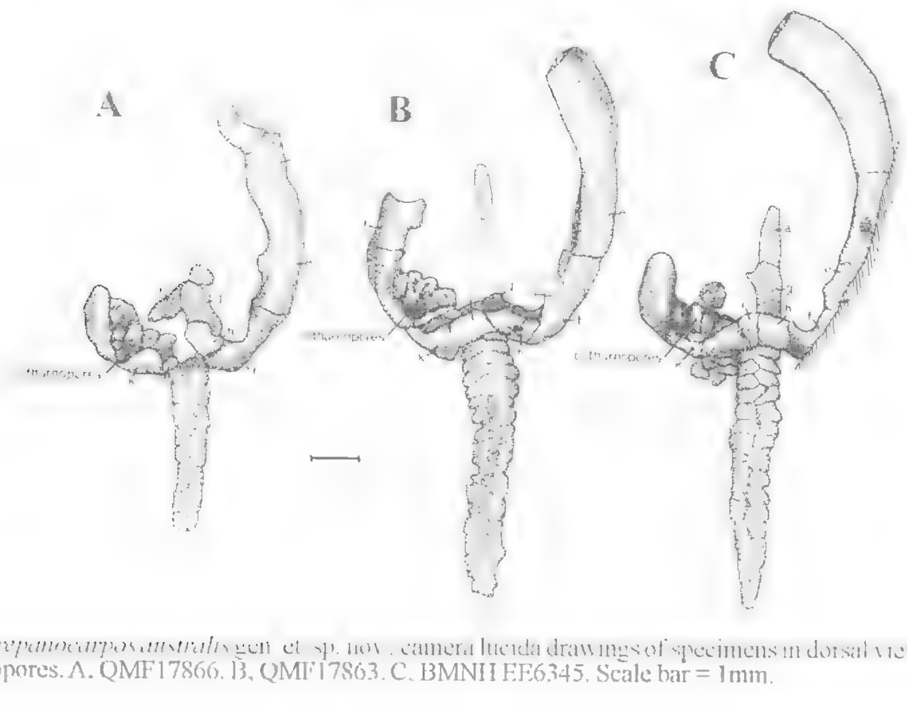


FIG. 6. *Drepanocarpos australis* gen. et sp. nov., camera lucida drawings of specimens in dorsal view showing cothurnopores. A, QMF17866. B, QMF17863. C, BMNH EE6345. Scale bar = 1mm.

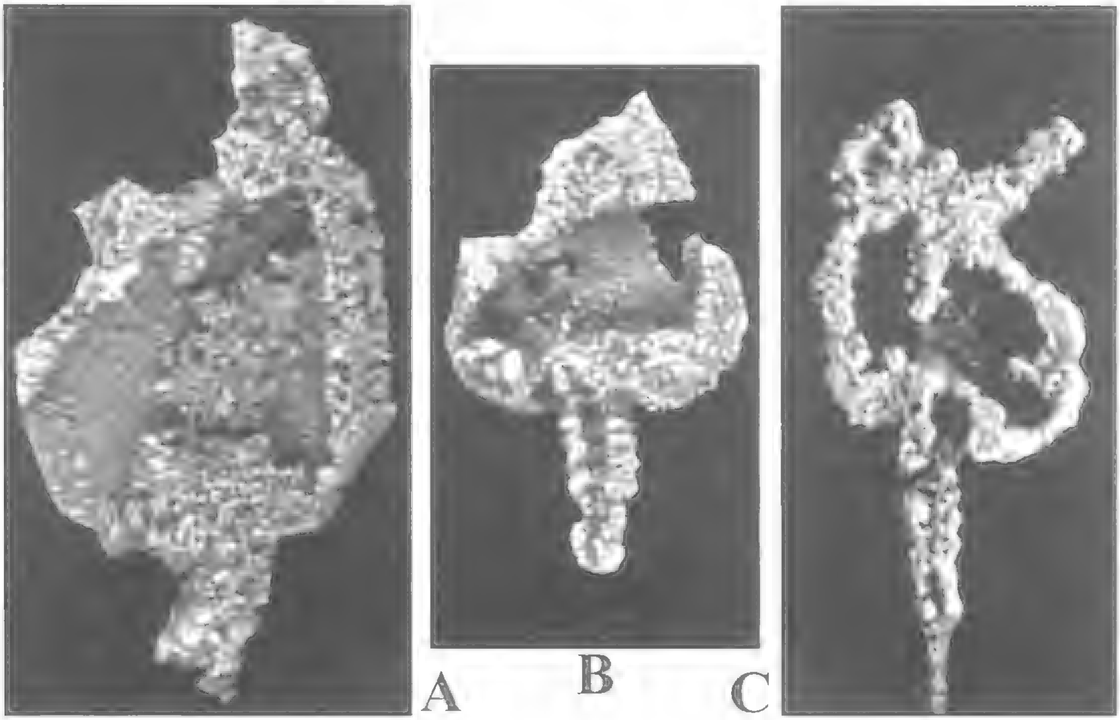

FIG. 7. *Drepanocarpos australis* gen. et sp. nov. A, QMF17867 in dorsal aspect, ×10. B, QMF17865 in dorsal aspect showing fully plated ventral surface, ×10. C, BMNH EE6346, in ventral view, ×12.

the posterior edge running between plates l and k. Unfortunately the ventral plating is unknown and we do not know whether plates a and c are united to form a transverse bar behind the buccal area as in *Drepanocarpos*.

*Archaeocothurnus* Sumrall et al., 1997 from the Middle and Upper Cambrian of Utah and Nevada, and including '*Phyllocystis*' (Ubaghs, 1963), differs from *Drepanocarpos* in that plate g is reduced to a narrow strut and there is a plated dorsal tegmen. This genus is thus more closely comparable to *Cothurnocystis*.

*Acuticarpus* Sumrall et al. (1997) from the Upper Cambrian of Wyoming is distinguished by its triangular shape, the more slender marginal plates, presence of a stylocone and lack of spines along the thecal margin. Poor understanding of the anterior of the theca makes comparison more difficult.

There are some similarities, indicating affinity, between *Drepanocarpos* and *Hanusia* Cripps, 1989 from the Ordovician of Czechoslovakia, particularly in possession of the spike on plate l. However, that genus has an l-spike and an e-spike, very limited extension of marginals onto the ventral surface, virtually straight right thecal margin, elongate thecal shape, and probable cothurnopores on dorsal surface.

In summary *Drepanocarpos* appears to be distinct from Ceratocystidae and Cothurnocystidae and bears most resemblance to the Phyllocystidae in particular *Lobocarpus* and Sprinkle's (1976) Spence Shale stylophoran. We thus make tentative assignment to the Phyllocystidae in line with Ubaghs (1999) caution in assigning *Lobocarpus*.

**Drepanocarpos australis** sp. nov.
(Figs 1-9)

ETYMOLOGY. Latin *australis*, southern, the only cornute so far known from Australia.

MATERIAL. Holotype, QMF17860, paratypes QMF17861-17871 and BMNH EE6344-6346.

DIAGNOSIS. As for genus.

DESCRIPTION. Body up to 10mm long and 7mm wide. Appendage more than 10mm long in an individual with a 5.5mm long body (Figs 8C,

10A) generally shorter, abruptly truncated. Ventral surface flat, with left laterodistal margin deeply embayed at plate a, with right margin uniformly convex. Proximal margin slightly embayed close to the appendage.

The appearance of individuals varies with the extent of weathering. In better preserved specimens distal plates b and c appear as curved processes resembling appendages (Figs 1A, 2A, 3, 4), while in the holotype these 2 processes are connected distally, forming a continuous marginal frame (Figs 1B, 2B). Marginal frame of 7 plates possibly, with 2 dorsal and 2 ventral plates above and below the tail. Plate k embayed dorsally for cothurnopores; cothurnopores as narrow slits surrounded by plating (Figs 4, 5) or as deep notches (Fig. 2), partially underlain by a narrow ledge. Plate l with a short pointed spike not much longer than the thickness of the marginal frame. Plate boundaries on the marginal frame are very difficult to make out, especially anteriorly because of the coarseness of silicification and because the anterior is available in only 2 specimens. Plates a and c/d apparently abutting to form a transverse strut across the body. Plate c/d (these 2 plates are inferred but no separating suture can be discerned with certainty) long and curved, tapering distally, with short lateral bar distally; one specimen (Fig. 1B) suggests that a short lateral bar connects to plate b across the distal extremity of the body via a small plate. We do stress that this interpretation of a single specimen requires verification. Distal processes not present. Plates c/d, e and f forming a continuous smooth curved right-hand margin. Plate f with an internal notch proximally.

Dorsal plating best seen from the interior. Suture separating plates a and g evident; suture defining a V-shaped region towards the right. Other sutures not discernible; dorsal surface of a few large plates sutured together but the precise pattern of plate sutures is unknown. No large calcite plates are preserved distal to the transverse bar formed by plates a/c.

Ventral surface largely lost; small plates occasionally seen inside marginal frame may be the remains of a plated tegmen.

Cothurnopores 4 or 5, in the proximal angle of the head close to the marginal frame in the embayment of plate k (Figs 5, 6). Fine structure masked by preservation, apparently a row of closely spaced oval mounds, each with an irregular surface sometimes showing a median depression.

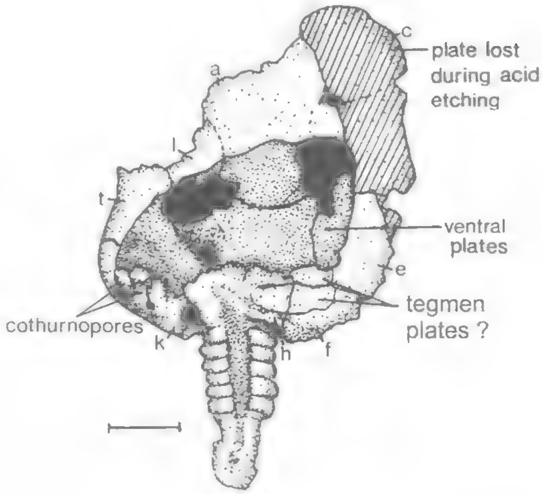


FIG. 8. *Drepanocarpos australis* gen. et sp. nov., camera lucida drawings of QMF17865 with plating interpretation. A, dorsal view. B, proximal view. Scale bar = 1mm.

Appendage of a thicker proximal part of 6 well-defined rings and a thinner distal part (whose structure is not well seen in any specimen). No specimen well enough preserved to show the stylocone.

REMARKS. Although 12 specimens of this species are known, none is sufficiently well-preserved to show all of the characteristic features. The reconstruction (Fig. 9) has therefore had to be composite. In particular plate sutures are often difficult to identify due to the coarse silica replacement, and sutures are only indicated if they appear consistenly in a number of specimens. The different extent of weathering also poses a problem of interpretation. However, enough is known about this species to show that it merits separation at generic level from other cornutes as discussed above under the generic heading.

The most closely related cothurnocystid is the unnamed solute from the Spence Shale, Utah (Sprinkle, 1976, pl. 1, fig. 1) which differs from *D. australis* in having a slightly broader head, no spike on plate l, a longer and better developed plate i and no apparent connection between plate a and c (though this may be a preservational artefact; the connection is not seen either in QMF17860). Furthermore, the Spence Shale cothurnocystid has a narrower, less blade-like right-hand margin.

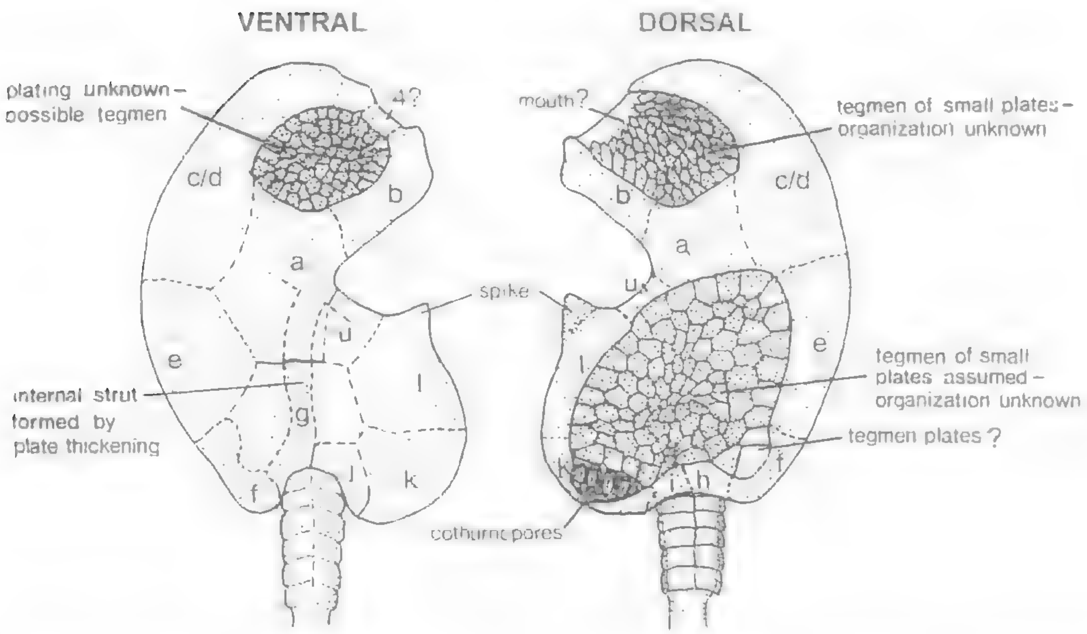


FIG.9. Possible reconstruction of *Drepanocarpos australis* gen. et. sp. nov. We stress that interplate sutures are not always clear and their representation with dashed lines indicates this uncertainty. The sketch is provided as the best estimate, though by no means certain, of the skeleton from available material.


## ACKNOWLEDGEMENTS

We are grateful to Dick Jefferies, Natural History Museum, London and Jim Sprinkle, University of Texas, Austin for strong reviews, acknowledging that neither referee necessarily agrees with all or any of the conclusions.


## LITERATURE CITED


CASTER, K.E., 1967. Homoiostelea. Pp. 581-623. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S, Echinodermata 1. (Geological Society of America & University of Kansas: New York).

CRIPPS, A.P. 1989. A new genus of stem chordate (Cornuta) from the Lower and Middle Ordovician of Czechoslovakia and the origin of bilateral symmetry in the chordates. Geobios 22: 213-245.

DERSTLER, K. 1979. Biogeography of the stylophoran carpoids (Echinodermata). Pp. 91-104. In Gray, J. & Boucot, A. (eds) Historical biogeography, plate tectonics and the changing environment (Oregon State University Press: Corvallis).

JAEKEL, O., 1901. Ueber Carpoiden, eine neue Klasse von Pelmatozoen. Zeitschrift der Deutschen geologischen Gesellschaft 52: 661-677.

JEFFERIES, R.P.S., 1986. The ancestry of the vertebrates. (British Museum (Natural History): London).

JEFFERIES, R.P.S., LEWIS, M. & DONOVAN, S.K., 1987. *Protocystites menevensis* — a stem-group chordate (Cornuta) from the Middle Cambrian of south Wales. Palaeontology 30: 429-484

JELL, P.A., BURRETT, C.F. & BANKS, M.R., 1985. Cambrian and Ordovician echinoderms from eastern Australia. Alcheringa 9: 183-208.

RUTA, M. & JELL, P.A.1999a *Protocytidium* gen. nov., a new anomalocystitid mitrate from the Victorian latest Ordovician and evolution of the Allanicytidiidae. Memoirs of the Queensland Museum 43: 353-376.

1999b. *Adoketocarpus* gen. nov., a new mitrate from the Ludlovian Kilmore Siltstone and Lochkovian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 377-398.

1999c. Two new anomalocystititid mitrates from the Lower Devonian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 399-422.

1999d. A note on *Victoriacystis wilkinsi* (Anomalocystitida, Mitrata) from the Upper Silurian of Victoria. Memoirs of the Queensland Museum 43: 423-430.

1999e. Revision of Silurian and Devonian Allanicytidiidae (Anomalocystitida, Mitrata) from southeastern Australia, Tasmania and New Zealand. Memoirs of the Queensland Museum 43: 431-451.

SHERGOLD, J.H., 1982. Late Cambrian trilobites from the Chatsworth Limestone, western Queensland

Bulletin of the Bureau of Mineral Resources Geology and Geophysics Australia 186: 1-111.

SMITH, A.B. & JELL, P.A. 1990. Cambrian edrioasteroids from Australia and the origin of the starfishes. Memoirs of the Queensland Museum 28: 715-778.

SPRINKLE, J. 1976. Biostratigraphy and paleoecology of Cambrian echinoderms from the Rocky Mountains. Brigham Young University Geology Studies 23(2): 61-73.

SUMRALL, C.D., SPRINKLE, J. & GUENSBURG, T.E. 1997. Systematics and paleoecology of Late Cambrian echinoderms from the western United States. Journal of Paleontology 71: 1091-1109.

UBAGHS, G. 1963. *Cothurnocystis* Bather, *Phyllocystis* Thoral and an undetermined member of the Order Soluta (Echinodermata, Carpoidea) in the uppermost Cambrian of Nevada. Journal of Paleontology 37: 1133-1142.

1969. Les échinodermes carpoïdes de l'Ordovicien inférieur de la Montagne Noire (France). (Cahiers de Paléontologie, éditions du Centre National de la Recherche Scientifique: Paris).

1999. Echinodermes nouveaux du Cambrien supérieur de la Montagne Noire (France Meridionale). Geobios 31: 809-829.

UBAGHS, G. & ROBISON, R.A. 1988. Homalozoan echinoderms of the Wheeler Formation (Middle Cambrian) of western Utah. University of Kansas Paleontological Contributions Paper 120: 1-17.

**ABERRANT *PANDANOCRINUS*, EARLY DEVONIAN CRINOID FROM NORTH QUEENSLAND.** *Memoirs of the Queensland* Museum *43(1): 351. 1999:- Pandanocrinus martinswellensis* Jell et al., 1988 was described from the Early Devonian (Pragian; *sulcatus* Biozone) Martins Well Limestone Member of the Shiels Creek Formation at Martins Well on Pandanus Creek Station, north Queensland. Collections from the type locality in the University of Queensland (UQL3579) and the Queensland Museum (QML550) include several hundred individuals with uniform plate arrangement except for QMF25736, which has 7 plates in the radial circlet and a small triangular plate at the D-E interray between basal and radial circlets.

BB 3, equal, 2 with 3 sides against RR, 3rd with 4 or 5. BB circlet 7-sided; sides are not even either in length or in angle of meeting. Orientation is difficult because free arms and most of the upper theca are missing, only a few fixed brachials and interbrachials preserved. 7-sided anal plate bisected by diameter with one of the interplate sutures in the basal circlet indicating A ray-CD interray line of symmetry. Other interplate basal circlet sutures in C & D rays; in normal specimens the sutures are in the A, C and E rays (Jell et al., 1988). With this orientation (Fig. 1B) A, B and C rays appear normal although the upper margin of the B radial is not symmetrical. D & E rays are irregular in plate arrangement and shape. D & E radials appear to be divided, each into 2 plates of comparable size; thus the 7 radials. Between adjacent D and E radials (i.e. 1 from each pair) and resting on the basal circlet is a small triangular plate which has no homologue in other crinoids. If the D radial is correctly interpreted as being 2 plates then the anal is not in contact with the C radial as in normal specimens. Moreover, there appear to be 2 plates in the CD interray in the 1st brachial circlet; thus producing a circlet of 11 rather than the normal 10 plates. Apart from the more numerous plates the shapes of most posterior plates from the C to E rays are irregular. This is clearly a unique specimen. The most obvious explanation involves traumatic injury as a juvenile; growth centres of several plates were fragmented and 2 plates grew where formerly there had been 1. In radials, division was fairly equal whereas the small triangular plate must have had only a tiny piece of growth centre to start it off. Alternative explanations could involve a growth response to a constricted growth position (e.g., in a crevice or, given the number of fossils at the site, in a tightly packed meadow of large crinoids) or a single mutation. The chance of 1 mutation dividing 4 or more growth centres is remote and dismissed here. The influence of the surroundings could affect overall shape and symmetry but is unlikely to have induced growth of entirely separate plates.

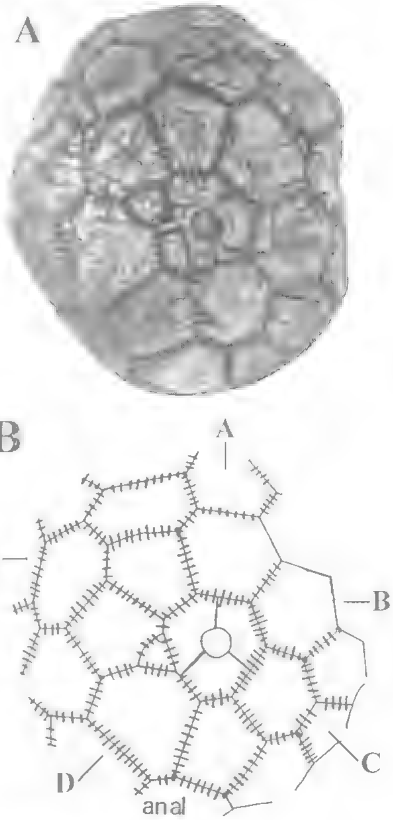


FIG. 1. *Pandanocrinus martinswellensis* Jell et al., 1988. A, basal view of aberrant theca QMF25736, ×1.5. B, plate diagram of QMF25736.

## Literature Cited

JELL, P.A., JELL, J.S., JOHNSON, B.D., MAWSON, R. & TALENT, J.A. 1988. Crinoids from Devonian limestones of eastern Australia. Memoirs of the Queensland Museum 25(2) 355-402

*Peter A. Jell, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia; 17 May 1999.*

**THE CRINOID *MELOCRINITES TEMPESTUS* IN THE DEVONIAN CAMPWYN BEDS ON THE SHORE OF REPULSE BAY, SOUTH OF PROSERPINE.** *Memoirs of the Queensland Museum 43: 352. 1999*:- Along the western shores of Repulse Bay, just south of Proserpine, the Campwyn Volcanics (Fergusson et al., 1994) extend from around Seaforth in the south to near Lethebrook in the north (Paine, 1972). About midway between Midgeton and Lethebrook, in the vicinity of the Laguna Quays Resort (termed Aqua del Rey in Fergusson et al., 1994), the Campwyn Volcanics outcrop in a broad intertidal band more than 100m wide. Strike is virtually parallel to the waterline and dip is to the west at very low angles. Muddy volcanoclastic limestones predominate with the percentage bioclasts highly variable between beds. In a few of these beds crinoidal and other shelly (including coral and brachiopod) debris is common; sections of stem up to 100mm long and 10mm in diameter are common. Cup and arm plates are rare. In 1991 Mr Bob Spencer forwarded the crinoid calyx figured herein to the Queensland Museum after having collected it in the intertidal area now disturbed by excavations for the Laguna Quays Resort; he also sent a badly weathered specimen of a large pleurotomariacean gastropod and a solitary rugose coral. Subsequent collection by the author has confirmed the provenance but failed to discover any further identifiable crinoids.

This crinoid (Queensland Museum Fossil 40967), with a high conical, smooth cup, 52mm long, is identified as a very large specimen of *Melocrinites tempestus* Jell et al., 1988. This assignment is based on the shape, arrangement and ornament of cup plates and cup shape. The specimens figured by Jell et al. (1988) are mostly weathered smooth but one (Jell et al., 1988, fig. 13G) shows the corners of cup plates depressed indicating that the unweathered cup had strongly convex plates as in the Campwyn Volcanics specimen.

The age of the Campwyn Volcanics has been given as Upper Devonian based on corals determined by Hill from near Seaforth (Jensen et al., 1966; McKellar in Roberts et al., 1971) and Lower Carboniferous based on brachiopods from the Mackay sheet, determined by McKellar (Jensen et al., 1966). In the Proserpine sheet area the age has been given as Upper Devonian based on the Seaforth corals (Paine, 1972) or on conodonts in samples from the Laguna Quays locality (Fergusson et al., 1994, fig. 3b). However, the crinoid species determined herein has previously only been found in the Middle Devonian (Givetian) part of the Papilio Formation of the Broken River Province. *Melocrinites* is widely recorded from the Silurian to Frasnian in the Northern Hemisphere and Australia but is only recorded from the Famennian in New York. The only Australian Frasnian record is in the Canning Basin reef complex (Jell & Jell, 1999). Since the conodont age suggested for this locality is Famennian (R.A. Henderson pers. comm. 1999) there appears to be some conflict with the crinoidal indication. This single crinoid could be a long ranging species providing a second Famennian occurrence for the genus or far less likely the section at Laguna Quays could represent a longer period of time than previously thought.

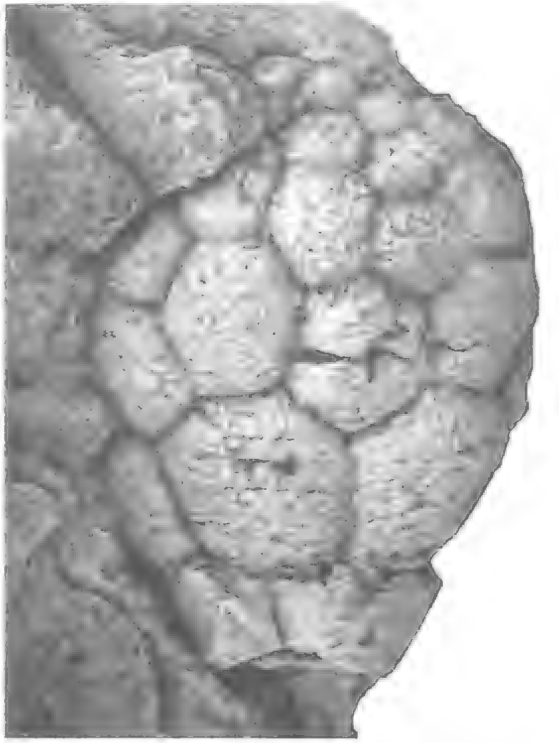

FIG. 1. *Melocrinites tempestus* Jell et al., 1988, lateral view of cup QMF40967, ×1.5

**Literature cited**

FERGUSSON, C.L., HENDERSON, R.A. & WRIGHT, J.V. 1994. Facies in a Devonian-Carboniferous volcanic fore-arc succession, Campwyn Volcanics, Mackay district, central Queensland. Australian Journal of Earth Sciences 41: 287-300.

JELL, P.A. & JELL, J.S. 1999. Crinoids, a blastoid and a cyclocystoid from the Upper Devonian reef complex of the Canning Basin, Western Australia. Memoirs of the Queensland Museum 43: 201-236.

JELL, P.A., JELL, J.S., JOHNSON, B.D., MAWSON, R. & TALENT, J.A. 1988. Crinoids from Devonian Limestones of eastern Australia. Memoirs of the Queensland Museum 25: 355-402.

JENSEN, A.R., GREGORY, C.M. & FORBES, V.R. 1966. Geology of the Mackay 1:250000 sheet area, Queensland. Bureau of Mineral Resources, Geology and Geophysics Report 104:1-58.

PAINE, A.G.L. 1972. Proserpine Qld. Sheet SF/55-4 1:250000 Geological Series - Explanatory Notes (including map) 24p.

ROBERTS, J., JONES, P.J., JELL, J.S., JENKINS, T.B.H., MARSDEN, M.A.H., McKELLAR, R.G., McKELVEY, B.C. & SEDDON, G. 1971. Correlation of the Upper Devonian rocks of Australia. Journal of the Geological Society of Australia 18(4): 467-490.

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# *PROTOCYTIDIUM* GEN. NOV., A NEW ANOMALOCYSTITID MITRATE FROM THE VICTORIAN LATEST ORDOVICIAN AND EVOLUTION OF THE ALLANICYTIDIIDAE

MARCELLO RUTA AND PETER A. JELL

Ruta, M. & Jell, P.A. 1999 06 30: *Protocytidium* gen. nov., a new anomalocystitid mitrate from the Victorian latest Ordovician and evolution of the Allanicytidiidae. *Memoirs of the Queensland Museum* 43(1): 353-376. Brisbane. ISSN 0079-8835.

The anomalocystitid mitrate *Protocytidium elliottae* gen. et sp. nov. is described from the uppermost Ordovician Darraweit Guim Mudstone in central Victoria. *Protocytidium* has: 1) 12 plates on the convex surface, with only 3 in distal row and the remaining 9 as in *Enoploura*; 2) remarkably asymmetrical lateral and median orifice plates of plano-concave surface divided into a 'thecal' portion framing the body orifice and a 'lip' projected distally beyond the orifice; 3) much reduced plate B failing to contact right LOP; 4) narrow, elongate plate A sutured with proximal 2/3-3/4 of medial margin of left intermediate lateral marginal plates; 5) short, slender, almost straight left spine and longer, more robust, convex, sickle-shaped right spine; 6) cancellate to honeycomb-like stereom, often replaced by radiating trabeculae near periphery of plates; 7) styloid trapezoidal, bearing semicircular styloid blades with radiating trabeculae; 8) proximal blade about half as large as distal blade. *Protocytidium* is intermediate between *Enoploura popei* and the basal allanicytidiid *Occultocystis koeneni*. The Allanicytidiidae are reviewed in the light of this new find. □ *Protocytidium, Anomalocystitida, Allanicytidiidae, Bolindian, Victoria.*

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During field mapping of the Kilmore 1:50,000 sheet (Vandenberg, 1992), which included a study of Ordovician/Silurian boundary sections in the Deep Creek and Ben Dhui Creek areas (Vandenberg et al., 1984), numerous specimens of a small mitrate were discovered at NMVPL660 in Ben Dhui Creek (Vandenberg et al., 1984, figs 1, 2A). This species has a combination of skeletal features making it transitional between *Enoploura* Wetherby, 1879 from the Middle to Late Ordovician of North America (Caster, 1952; Parsley, 1991) and the allanicytidiid *Occultocystis koeneni* Haude, 1995 from the Lower Devonian of Argentina. The new taxon is the oldest and only Ordovician member of the Allanicytidiidae. In this paper we describe and reconstruct the taxon, assess its phylogenetic position and discuss its bearing on the origin and evolution of the Allanicytidiidae.

## GEOLOGICAL SETTING

The material described herein comes from NMVPL660 (Vandenberg et al., 1984, fig. 2A, appendix 2). It is in the bed of Ben Dhui Creek, 750m N of the Wallan to Woodend road, about 10km W of Wallan at AMG311740-5860360 on the Kilmore 1:50,000 sheet 7823-II Series R 754, Edition 1-AAS (1979). It is in the type section of the Darraweit Guim Mudstone which consists of medium to thick bedded massive calcareous mudstone. The mudstone is black when fresh but surface exposures are usually decalcified, weathered and grey or green as at NMVPL660. The associated fauna, which is preserved in situ, includes the trilobite *Songxites darraweitensis* (Campbell), the graptolite *Climacograptus angustus* Perner and nautiloids. This is a thin unit (20m in the type section) precisely dated by the widespread graptolite *Climacograptus? extraordinarius* (Sobolevskaya) which occurs in the youngest Ordovician Zone at the top of the Bolindian Stage.

## SYSTEMATIC PALAEONTOLOGY

Anatomical terminology and plate nomenclature (Appendix) follow Ruta (in press), Ruta & Bartels (1998, fig. 5A,B) and Ruta & Jell (1999a,b,c). Specimens are housed in the Museum of Victoria, Melbourne (NMVP) wherein the locality is also registered (NMVPL). All photographic illustrations are of latex casts taken from decalcified moulds and whitened with ammonium chloride sublimate.

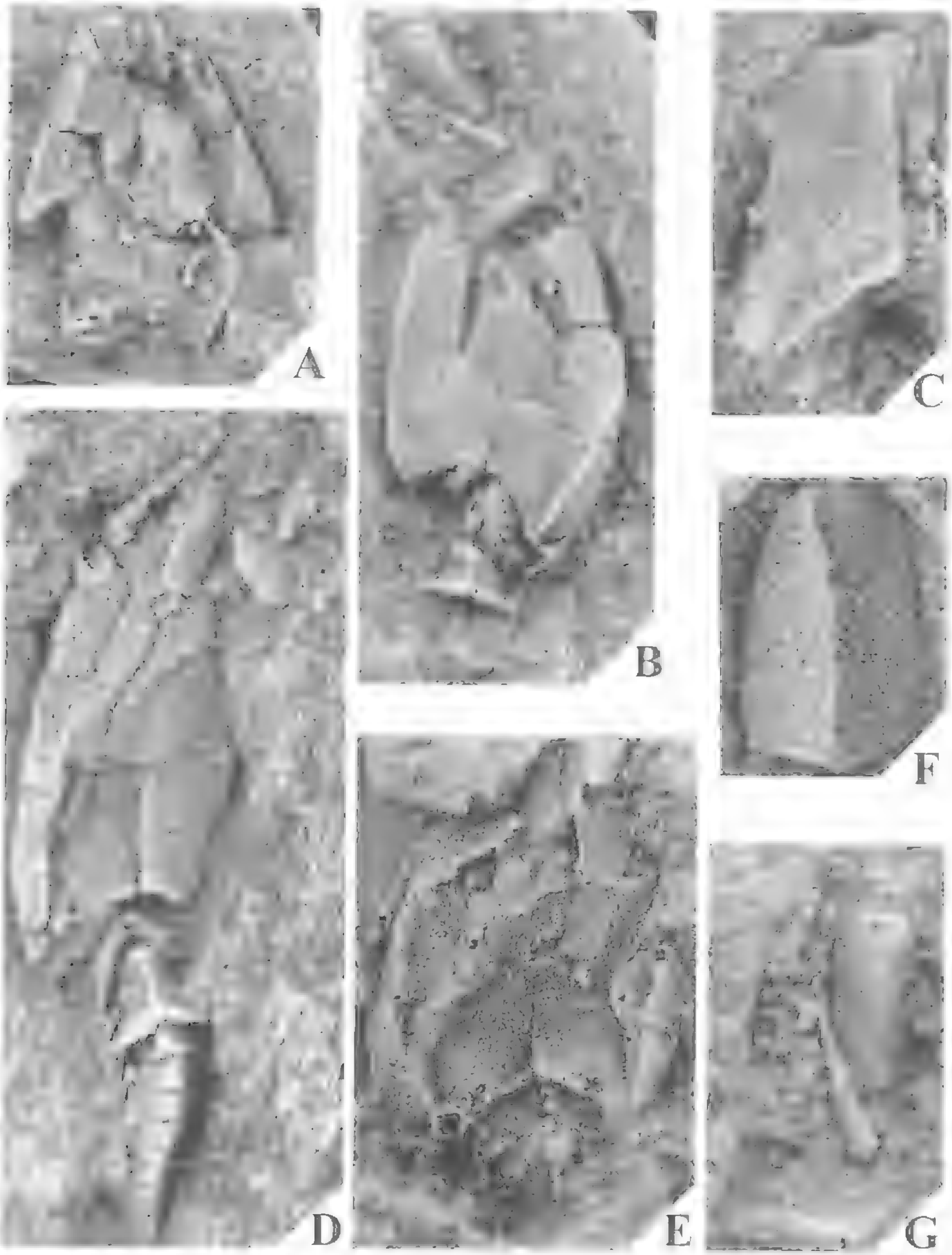


FIG. 1. *Protocytidium elliottae* gen. et sp. nov. A, inside of proximal part of convex surface and distal part of plano-concave surface of NMVP100439, ×5. B, G, partial plano-concave surface and detail of adjacent isolated spine (probably right spine) of NMVP100424, ×5 and ×7, respectively. C, fragment of marginal plate from plano-concave surface showing stereom fabric, NMVP100405, ×11. D, partial plano-concave surface and appendage, NMVP100401, ×5.5. E, partial plano-concave surface of NMVP100415, ×9. F, fragment of marginal plate from plano-concave surface showing stereom fabric, NMVP100400, ×11.

Class STYLOPHORA Gill & Caster, 1960
Order MITRATA Jaekel, 1918
Suborder ANOMALOCYSTITIDA
Caster, 1952
Family ALLANICYTIDIIDAE
Caster & Gill, 1967

DIAGNOSIS (modified from Caster & Gill, 1967; Caster, 1983; Haude, 1995; Ruta, in press). Median orifice plate (MOP) longer than each lateral orifice plate (LOP). Spines longer than distal margin of plano-concave surface. Distal part of convex surface of 3 or, more frequently, 2 plates with transverse thickening along inside of their distal margins. Distal styloid blade inclined proximally, sometimes with lateral ear-like projections. Sharp, longitudinal keel on external surface of styloid, failing to reach free margin of proximal blade (only in basal allanicytidiids). Proximal blade semicircular.

REMARKS. Ruta (in press) amended and expanded the diagnosis of the Allanicytidiidae, formalising Haude's (1995) proposal to include *Occultocystis koeneni*. As discussed below, some characters supporting the sister-group relationship between the new anomalocystitid and the Allanicytidiidae sensu Haude (1995) are diagnostic of the latter (Ruta, in press). Our diagnosis is, therefore, more generalised than those of Haude (1995) and Ruta (in press) and aims to avoid the problem of defining the Allanicytidiidae mainly on the basis of the simplified plating of the convex surface in the most derived representatives of the group (Caster, 1956, 1983; Caster & Gill, 1967; Philip, 1981; Ruta & Theron, 1997; Ruta & Jell, 1999c). However, reversal of some of the characters listed above occurs to some extent within the Allanicytidiidae.

**Protocytidium** gen. nov.

TYPE SPECIES. *Protocytidium elliottae* sp. nov.

ETYMOLOGY. Greek *proto*, the first and *cytidium*, a small box. Neuter.

DIAGNOSIS. Body subelliptical to pyriform, rarely subrectangular. Convex surface of 12 plates, with 3 in distal row. Medial and lateral orifice plates of plano-concave surface asymmetrical, divided into a 'thecal' portion framing the body orifice and a 'lip' projected distally beyond the orifice. Plate B reduced, not in contact with right lateral orifice plate. Plate A narrow, elongate. Left spine short, slender, almost straight; right spine longer, more robust, convex, sickle-shaped. Stereom cancellate to honeycomb-like, often replaced by radiating trabeculae near periphery of plates. Styloid trapezoidal, with semicircular blades with radiating trabeculae; proximal blade c.1/2 as large as distal blade.

REMARKS. The phylogenetic position of this new genus is discussed after the specific treatment below but simple distinguishing features are as follows: it differs from all anomalocystitids in the arrangement of the median and lateral orifice plates of the plano-concave surface, shape of the spines and elongate plate A with tiny plate B. *Enoploura* has 5 plates in the distal row on the convex surface, larger C21, different ornament and less expanded styloid. *Occultocystis* has C21 isolated from the proximal body margin, very few plates in the convex surface and C11 and C13 as marginal plates. Most of the advanced genera of the Allanicytidiidae are distinguished by having only C1 and C5 in the distal row on the convex surface, by having straight spines and more elaborate surface ornament.

**Protocytidium elliottae** sp. nov.
(Figs 1-14)

ETYMOLOGY. For Tracey Elliott of the Palaeontology Department at the Natural History Museum, London.

MATERIAL. Holotype: NMVP100401. Paratypes: NMVP100390-100400, 100402-100403, 100405-100406, 100408-100419, 100421-100436, 100438-100439, 100487-100488 all from NMVPL660.

DIAGNOSIS. As for genus.

DESCRIPTION. EXTERNAL. *Measurements*. Holotype (Fig. 1D): 11mm long, 6mm wide. Largest specimen (Fig. 7C): 14mm long, 7mm wide.

*Plano-concave surface* (Figs 1A-B,D-E, 2B-D, 4A-B, 6D, 7A,D, 8A, 9B, 10D, 13A). Mostly flat, except for slightly raised lateral margins, with lateral marginal plates divided more or less equally into subhorizontal and vertical parts. Lateral body walls of uniform depth, except for rapid tapering near proximal and distal ends (Fig. 13C-E). PM usually 1.5 times as wide proximally as distally, with straight to concave lateral margins on either side of slight lateral projection just proximal to midlength, with proximal margin strongly embayed for insertion of appendage. PLM with subhorizontal part subtriangular, with convex lateral margin and straight or broadly concave distal margin. ILM as long as PLM,

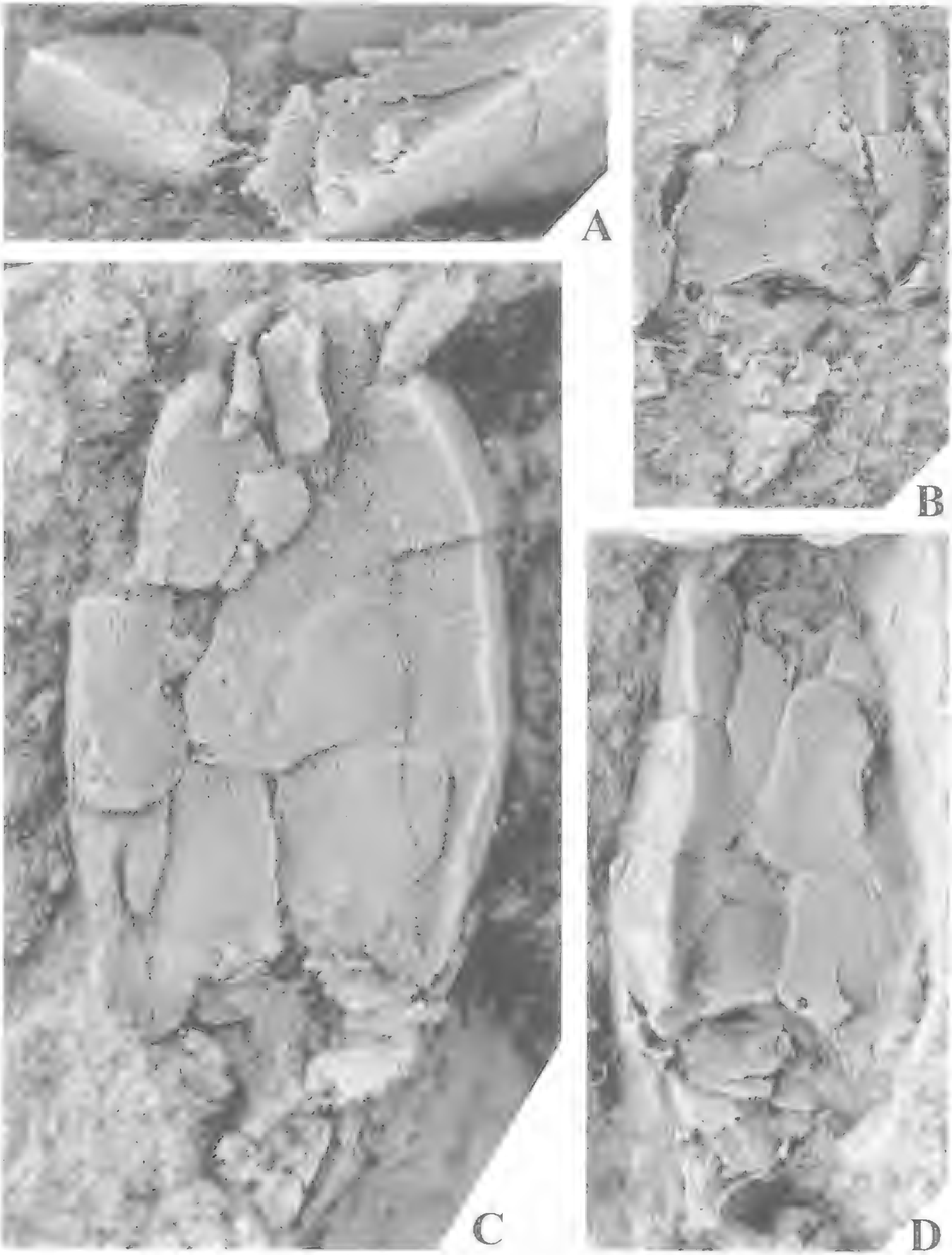


FIG. 2. *Protocytidium elliottae* gen. et sp. nov. A, distal view of distolateral corner of body NMVP100391, ×12. B, partial plano-concave surface of NMVP100397, ×10. C, plano-concave surface incomplete distally. NMVP100410, ×10. D, partial plano-concave surface of NMVP100403, ×7.

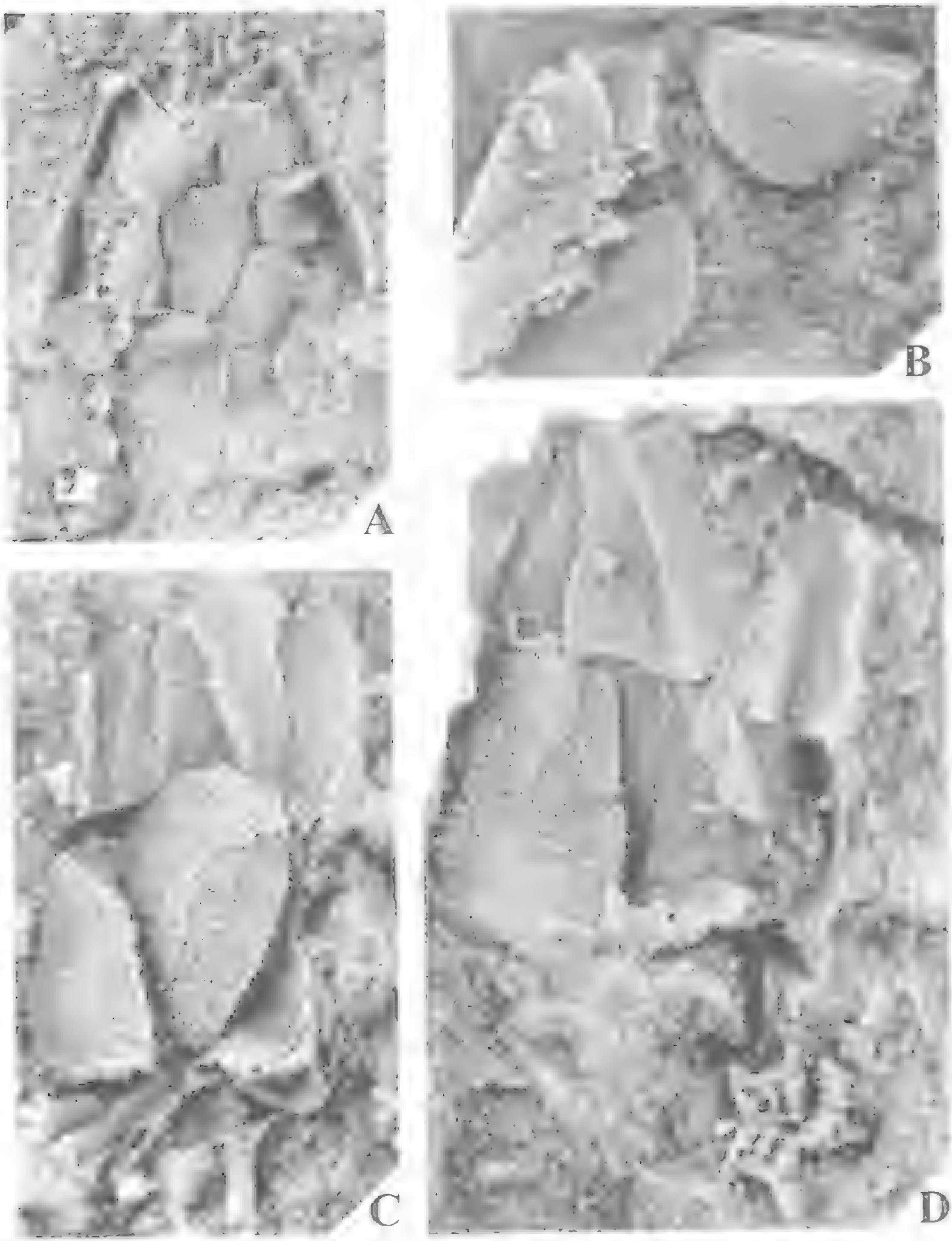


FIG. 3. *Protocytidium elliottae* gen. et sp. nov. A, convex surface of NMVP100488, ×7. B, distolateral corner of mostly disarticulated plano-concave surface of NMVP100391, ×11.5. C, partial proximal convex surface with inside of plano-concave surface in background, NMVP100390, ×6. D, inside of plano-concave surface with C21 still in position and with abapical surface of styloid in lower right, NMVP100417, ×11.5.

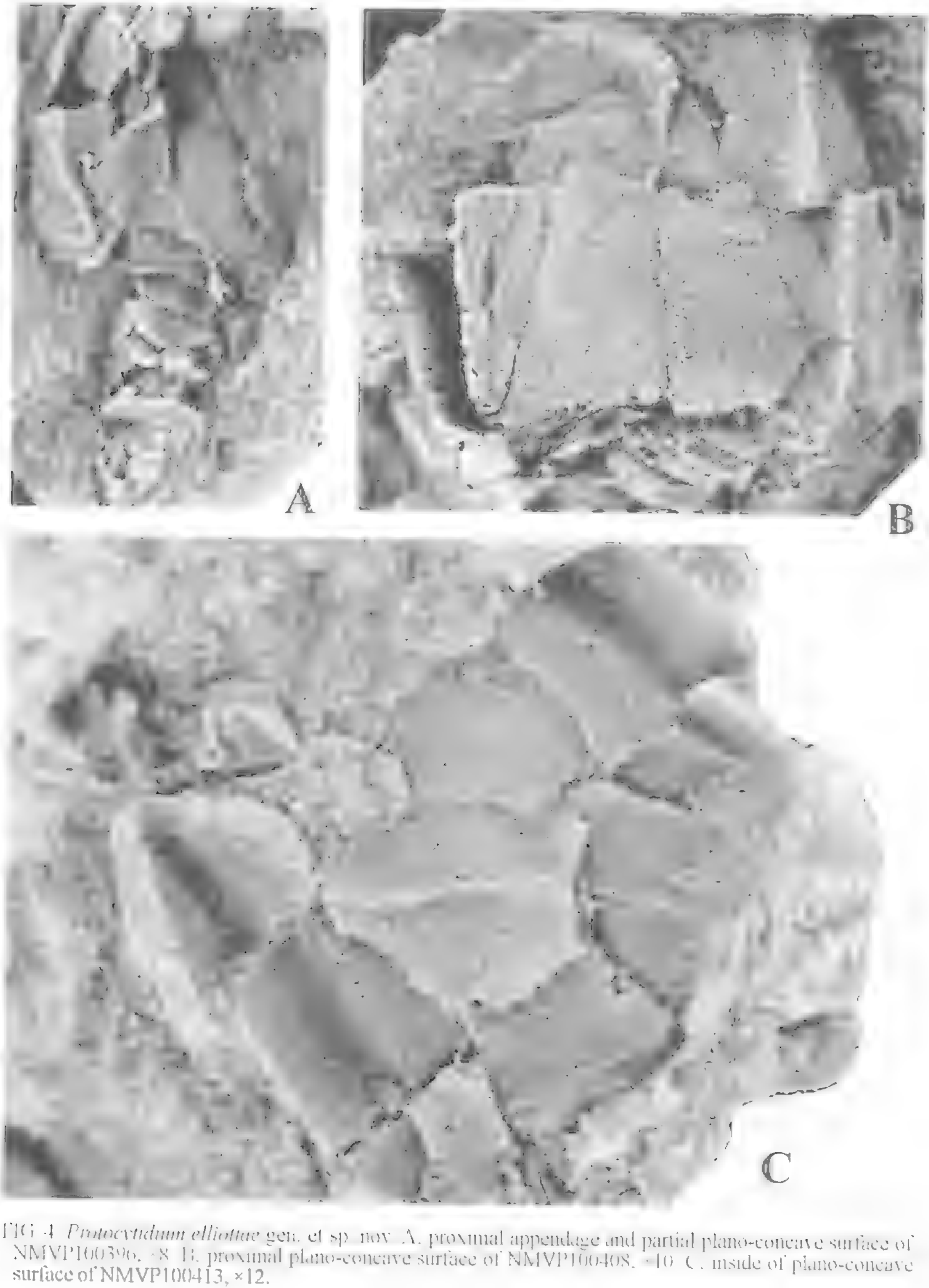


FIG. 4. *Protocytidium elliottae* gen. et sp. nov. A, proximal appendage and partial plano-concave surface of NMVP100396, ×8. B, proximal plano-concave surface of NMVP100408, ×10. C, inside of plano-concave surface of NMVP100413, ×12.

subrectangular, with medial margin of right ILM sigmoidal and medial margin of left ILM similarly sigmoidal distal to its junction with the A-C suture and proximally straight, with lateral and distal margins straight. DLM as long as ILM, subrectangular to subtrapezoidal, with shallow distal surface deepening laterally, with subcentral tubercle for spine articulation. LOP and MOP remarkably asymmetrical, at least twice as long as wide, divided into proximal 2/3 articulated with rest of plano-concave surface, and distal 1/3 projecting beyond distal margin of transverse orifice, usually giving rise to irregular process. Irregular gaps between distal parts of adjacent margins of orifice plates. Right LOP generally slightly shorter and narrower than left LOP or MOP.

Plate B subtrapezoidal (based on shape of available plate margins), sutured to left LOP, MOP, A and C. Plate A at least 5 times longer than wide, oblique to longitudinal body axis, sometimes remarkably shortened, with medial margin either gently convex or strongly convex in distal 1/2 and gently concave to straight in proximal 1/2, with pointed proximal wedged between C and left ILM. Plate C widening proximally, in contact with MOP.

*Convex surface.* All plates except C21 and C3 arranged in pairs (indicated by plate margins and by mirror image arrangement of medial and lateral plates sutured with C20-C22); distal 1/3 of convex surface invariably disrupted and poorly preserved.

C21 with width 40% of length, shield-shaped, with slightly convex longitudinal and transverse profiles; margins very gently convex except straight to weakly concave proximal margin, extreme proximolateral section also with short concave section, producing proximolateral projection. C20 and C22 subtrapezoidal, with maximum width proximally; transverse profile of plates strongly arcuate, especially near their proximo-lateral angle, with thickening immediately distal to proximal margin, with blunt proximo-lateral angles, with medio-distal angles proximal to latero-distal angles. C15 and C19 irregularly pentagonal, with greatest dimension at 45° to body axis, with proximo-medial margins in contact with latero-distal margins of C21, with sigmoidal medio-distal margins. C11 and C13 longer than wide, irregularly hexagonal, sutured along straight median suture. C6 and C9 subtrapezoidal, smallest plates of convex surface, lateral to C11 and C13, respectively. Distal 1/3 of convex surface poorly preserved in available material, but apparently consisting of 3 large plates in a transverse row (= C1, C3 and C5 based on comparison with *Enoploura* and *Occultocystis*). C5 (Fig. 3A) subrectangular, slightly longer than wide. C3 slightly longer than C5, subpentagonal.

*Body stereom and sculpture.* External surface of coarse stereomic fabric forming radial pattern on each plate. Terrace-like ridges and riblets absent. Stereom of thick, generally straight, sometimes bifurcating trabeculae often connected by irregularly spaced, short transverse bar-like connections; trabeculae and connections delimit deep pits and become more irregular and randomly branching near plate margins, where the pits are smaller, more numerous and polygonal. Trabeculae of proximal 1/2 of convex surface generally thicker than elsewhere.

C20-C22 (Figs 3A,C-D, 5C) with trabeculae almost parallel to each other, rarely bifurcating, gently arcuate or straight near lateral and medial margins of C20 and C22, becoming confluent near centre of proximal 1/2 of external surface of both plates, where they become slightly thicker and irregularly sinuous, with trabeculae on distal 1/2 thinner, subparallel to body axis, converging to centre of plates proximally. C21 with broadly arcuate trabeculae separated by granular fabric on proximal 2/3, with distal trabeculae straight, bifurcating, in fan-like arrangement. Remaining body plates with gradual changes in stereom structure from centre to periphery (Figs 1A-B,D-E, 2C-D, 4B, 7A-B,D, 8A-C, 9B, 10D); centre compact or honeycomb-like, with short, anastomosing trabeculae; more peripheral stereom of elongate trabeculae with transverse connections; surface with cancellate or honeycomb-like fabric proportional to plate size. Orifice plates with shallow pits and poorly defined, flat-topped trabeculae or coarse and without obvious surface pattern. Proximo-distally elongate trabeculae near proximal and distal margins of PLM, ILM and DLM (Fig. 1F-G). External surface of A and B (Fig. 1D) with large, widely spaced polygonal pits delimited by thin trabeculae. PM with honeycomb fabric, with radiating peripheral trabeculae, especially along distal margins.

*Spines.* Left spine straight or gently convex externally, round in cross-section, with clavate proximal end, with hemispherical articular surface, tapering distally, with blunt terminus. Right spine slightly longer and twice as wide as left spine, sickle-shaped, flattened except for

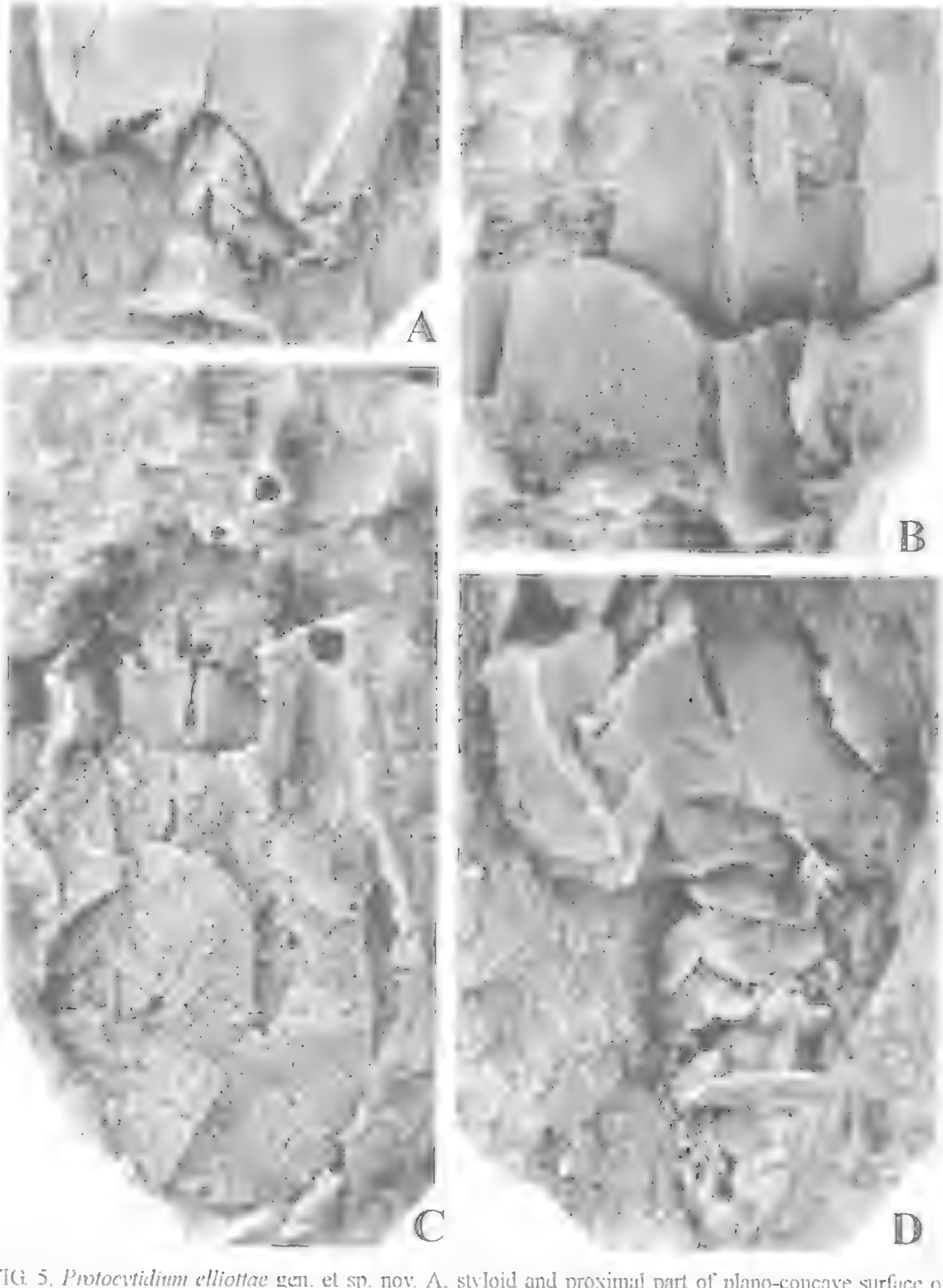


FIG. 5. *Protocytidium elliottae* gen. et sp. nov. A, styloid and proximal part of plano-concave surface of NMVP100424, ×8. B, inside of plano-concave surface of NMVP100423, ×12. C, partial convex suface with distal row removed to show inside of orifice plates of NMVP100398, ×12. D, proximal appendage and proximal plano-concave surface of NMVP100396, ×12.

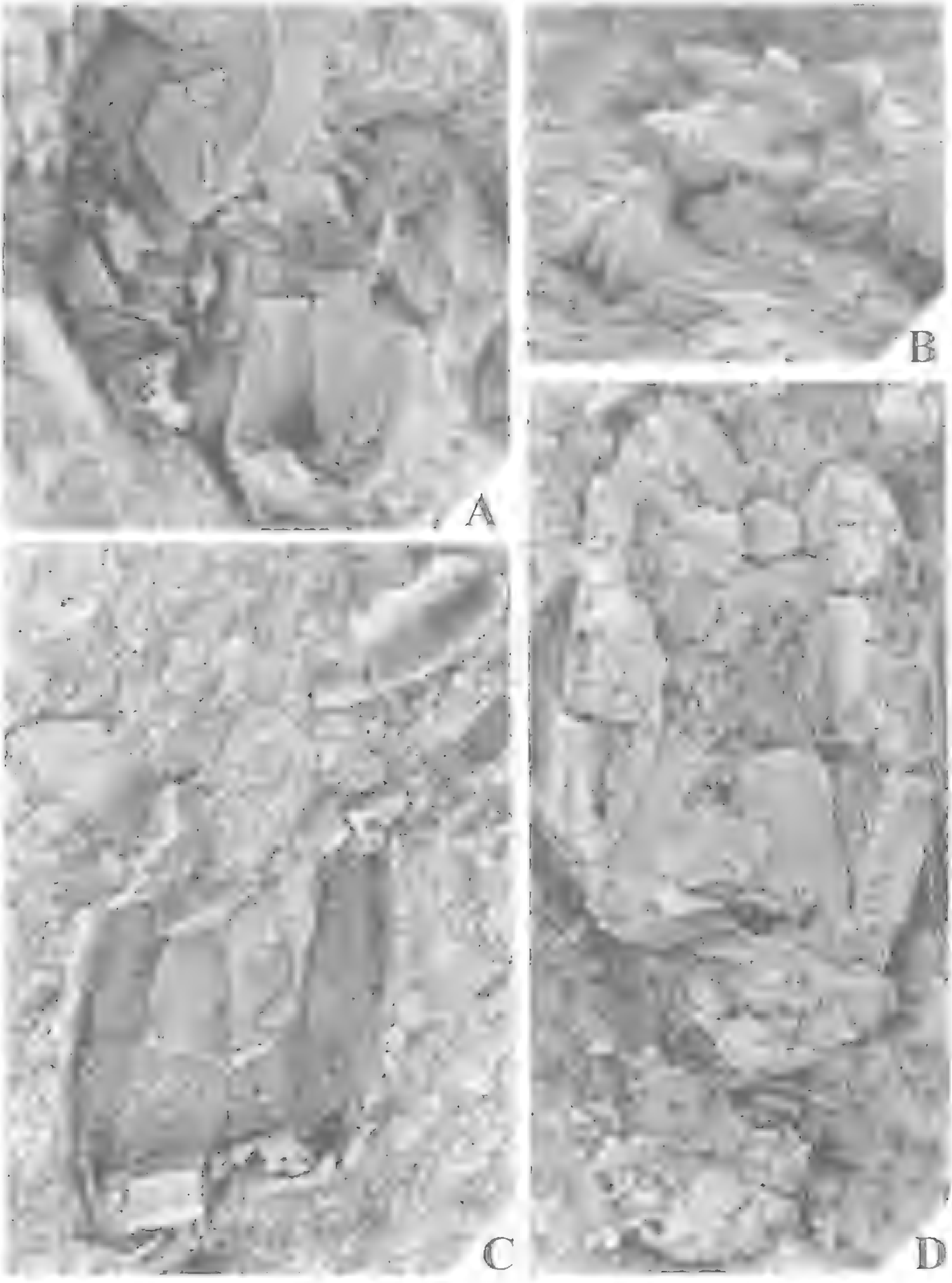

FIG. 6. *Protocytidium elliottae* gen. et sp. nov. A, inside of plano-concave surface of disarticulated NMVP100398, ×8. B, styloid of NMVP100430, ×12. C, inside of plano-concave surface of NMVP100487, ×7. D, plano-concave surface of NMVP100394, ×9.

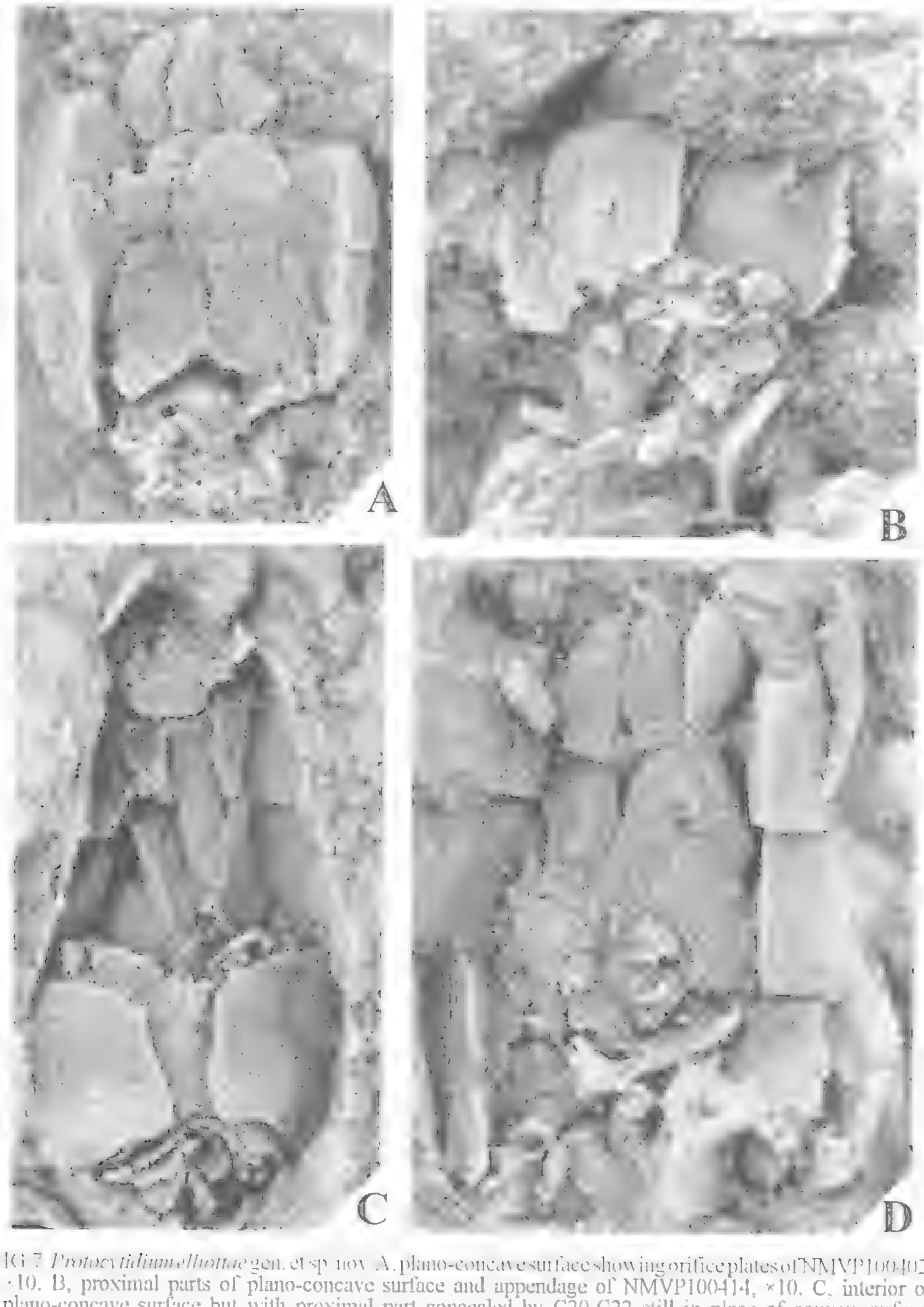


FIG. 7. *Protocystidium elliottae* gen. et sp. nov. A, plano-concave surface showing orifice plates of NMVP100402, ×10. B, proximal parts of plano-concave surface and appendage of NMVP100414, ×10. C, interior of plano-concave surface but with proximal part concealed by C20-C22 still in place of convex surface, NMVP100403, ×7. D, plano-concave surface with orifice plates intact, NMVP100395, ×9.

being conical distally, with sharp lateral and blunt medial margins, tapering distally to point, with subconical articular projection with 2 facets separated from short subcylindrical region by poorly pronounced ridge, with stereom of minute, irregular, shallow pits separated by coarsely granular to compact texture.

INTERNAL. *Plano-concave surface.* Internal surface of orifice plates divided into 2 unequal parts and different depths by transverse, distally concave thickening (Figs 7C, 8D, 9D, 11D, 12D). Internal surface of left latero-distal angle of body occupied by subtriangular area straddling suture between left DLM and left LOP and medial to tubercle for spine insertion on left DLM. Proximo-lateral 1/2 of subtriangular area slightly deeper and more raised than medio-distal 1/2 and delimited laterally and proximally by 2 ridges, continuing distally on internal surface of left LOP where the proximal, thicker ridge (pr in Fig. 12A) almost parallels the body axis, with the thinner ridge (lar in Fig. 12A) widening rapidly in its distal 1/2 before giving rise to thickened lateral margin of internal surface of left LOP, with central part of subtriangular area occupied by pit (p in Fig. 12A). Proximal and lateral ridges merging and continuing as a low sinuous ridge (lr in Fig. 12A) coinciding with junction between subhorizontal and vertical parts of plate. Distal 1/4 of low ridge with triangular lateral process (lp in Fig. 12A) partially delimiting shallow subelliptical area (sa in Fig. 12A). Low ridge of right side apparently fading gradually distally near medio-distal angle of internal surface of right ILM, immedialely lateral to point where the oblique septum (see below) straddles the suture between C and right DLM and abruptly changes direction. Oblique septum (se in Fig. 12C) with asymmetrical transverse section running from distal right angle to proximal left angle of inside of plano-concave surface (Figs 3C-D, 4C, 5B, 6A,C, 7C, 8D, 9A,C-D, 10C, 11A, 12C), with proximal 1/3 straight or gently convex to left, with proximal end merging into left scutula (sc in Fig. 12C). Left scutula transversely elongate (Figs 3D, 6A,C, 9C). Straight, transverse ridge (tr in Fig. 12C) (sensu Ruta & Jell, 1999a) delimited proximally by transverse furrow (tf in Fig. 12C). Second ridge, probably homologous with the proximal ridge of Ruta & Jell (1999a) (dr in Fig. 12C), running from left scutula to lateral margin of left PM, bending rapidly latero-distally and continuing on internal surface of left PLM as the most proximal part of the low ridge described above (lr in Fig. 12C). Apophyseal horns (ah in Fig. 12C) gently convex in transverse section, with straight proximal margin and gently convex distal margin in plan view, with medial ends separated by small gap (Fig. 9C). Septum (se) on plate C divided into a straight proximal 1/2 and narrower, gently convex to the right or sinuous distal half. Distal 1/3 of septum gently convex to the right, proximo-distal on inside of right DLM. Distally, septum has T-shaped birfucation near latero-distal angle of right DLM.

*Convex surface.* Inside of convex surface poorly preserved (Figs 1A, 11E). Co-operculum cup-like, just distal to midpoint of proximal margin of C20 and C22, with irregular rim, thicker in its distal 1/2 than in its proximal 1/2, with narrow slit at proximo-medial angle. Low oblique crest running medio-distally from medio-distal angle of co-opercular rim (Fig. 1A). C21 with weak struts radiating from point proximal to midlength (Fig. 1A) and reaching its proximal margin, with proximo-distally elongate, low, poorly defined ridge centrally (Fig. 11E), gradually disappearing distally.

*Stereom.* Inside of plano-concave surface with minute pits or, more frequently, honeycomb-like. Plate peripheries usually with minute pits sometimes very shallow and surrounded by poorly defined trabeculae. Proximal part of MOP and LOP compact or coarsely fibrillar, rarely with shallow, subelliptical pits and small lumps; distal part of orifice plates coarsely granular or with radiating and often bifurcating trabeculae separated by deep furrows (Figs 7C, 9D, 11D). Stereom of inside of convex surface cancellate to coarsely granular, of low anastomosing trabeculae separated by shallow elongate pits (Fig. 11E).

APPENDAGE. Proximal part of 6-7 tetramerous overlapping rings; ring plates of uniform width, in sutured contact mid-longitudinally and laterally. Ring plates on plano-concave side of body subrectangular, convex in transverse section, with straight proximal margins, with distal margins gently convex or sinuous and slightly thickened. Ring plates on convex side narrower, with straight proximal and distal margins. Styloid 3 times as wide as long, maximum width at distal blade, with low median keel. Proximal blade with semicircular, blunt free margin and flat to gently convex distal surface. Distal blade proximally recumbent, with semicircular sharp free margin, with flat surfaces, with proximal surface sometimes divided into 2 slightly convex halves (Figs 2B, 7B). Abapical surface of styloid (Figs 3D, 12E) gently concave

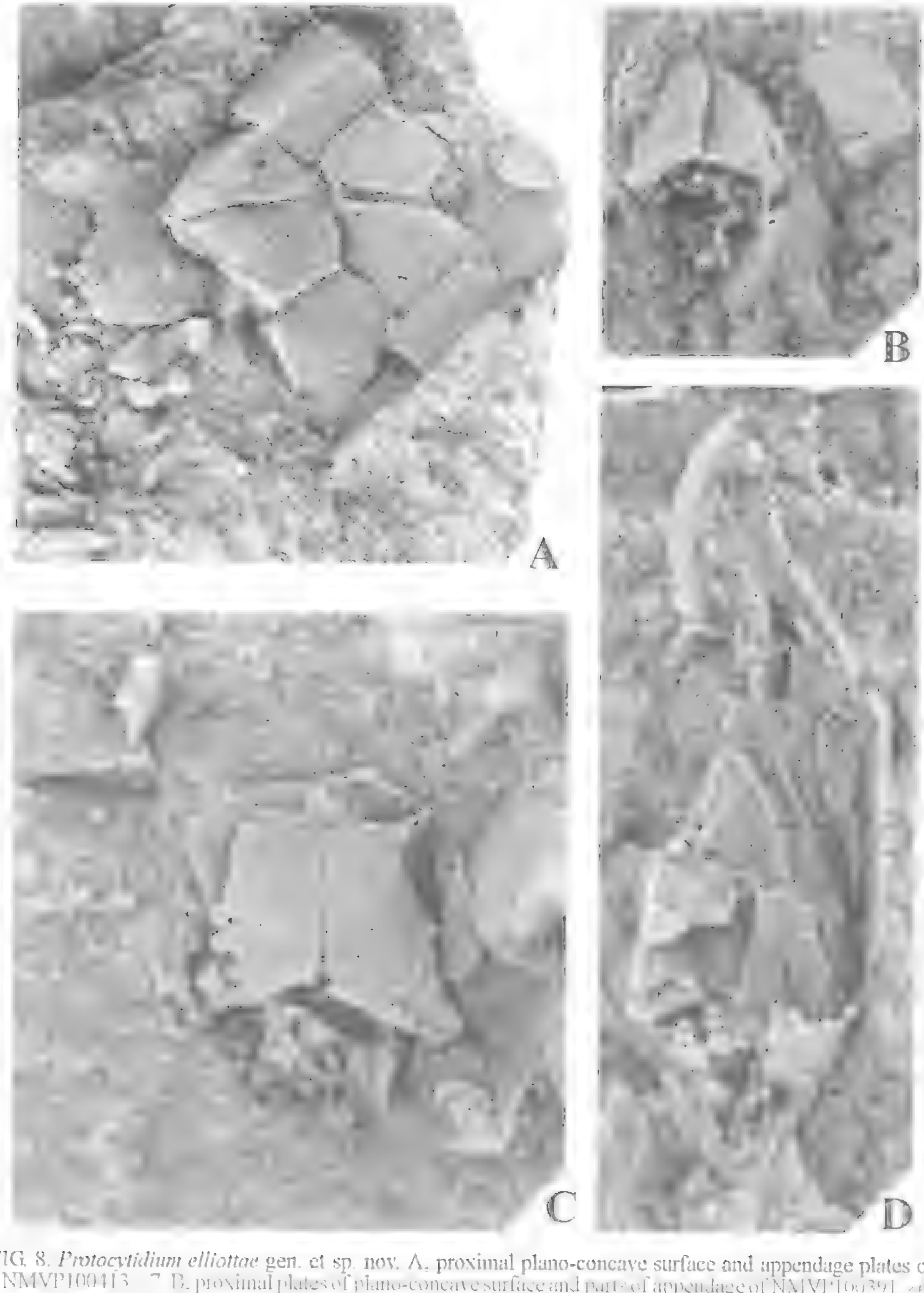


FIG. 8. *Protocytidium elliottae* gen. et sp. nov. A, proximal plano-concave surface and appendage plates of NMVP100413, ×7. B, proximal plates of plano-concave surface and parts of appendage of NMVP100391, ×6. C, PM plates over inside of convex surface plates of NMVP100419, ×12. D, inside of plano-concave surface of NMVP100401, ×12.

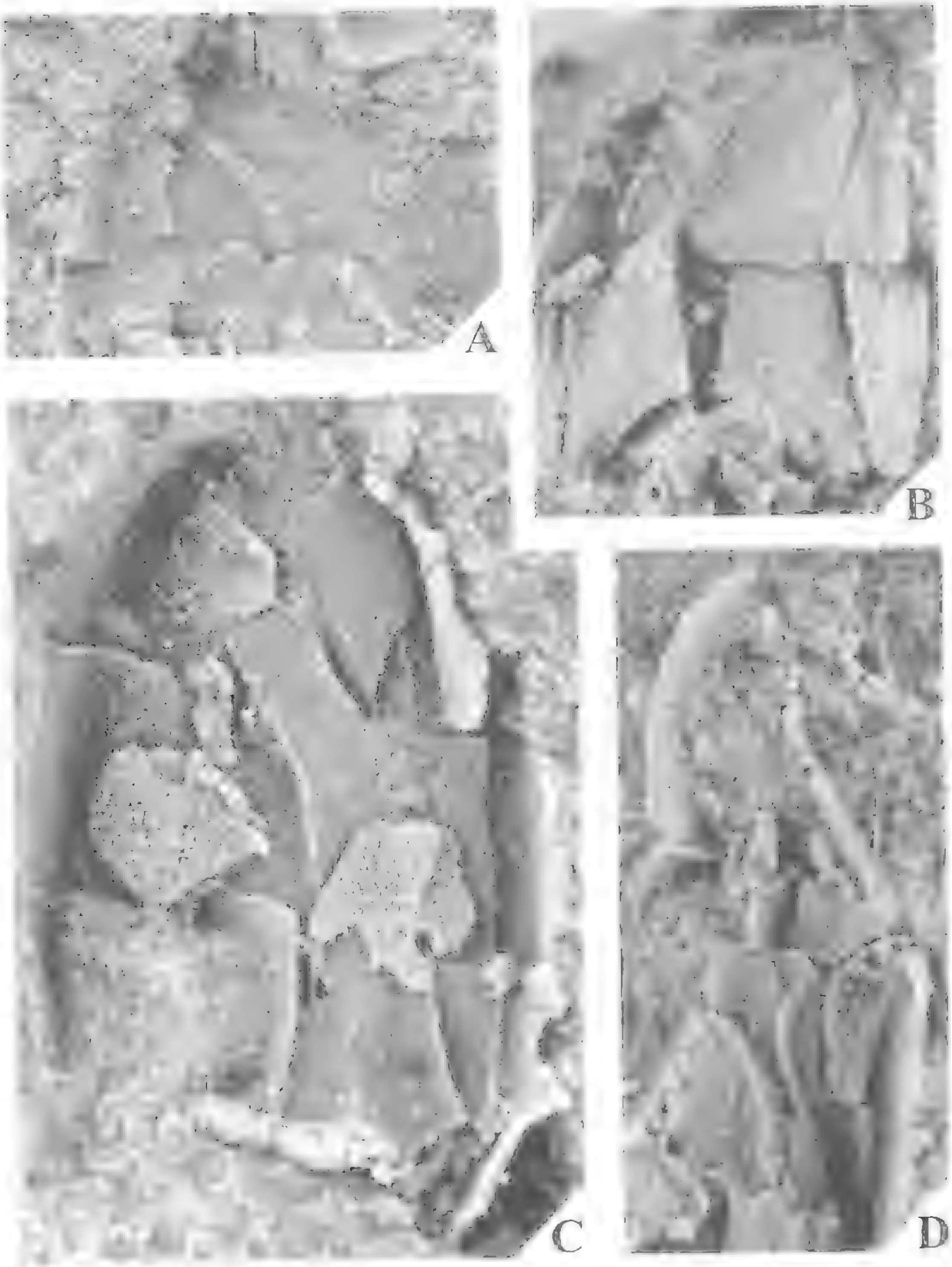


FIG. 9. *Protocytidium elliottae* gen. et sp. nov. A, inside of plano-concave surface and orifice plates of NMVP100392, ×7. B, partial plano-concave surface of NMVP100409, ×12. C, inside of plano-concave surface of NMVP100418, ×12. D, detail of distal part of Fig. 8D, NMVP100401, ×15.

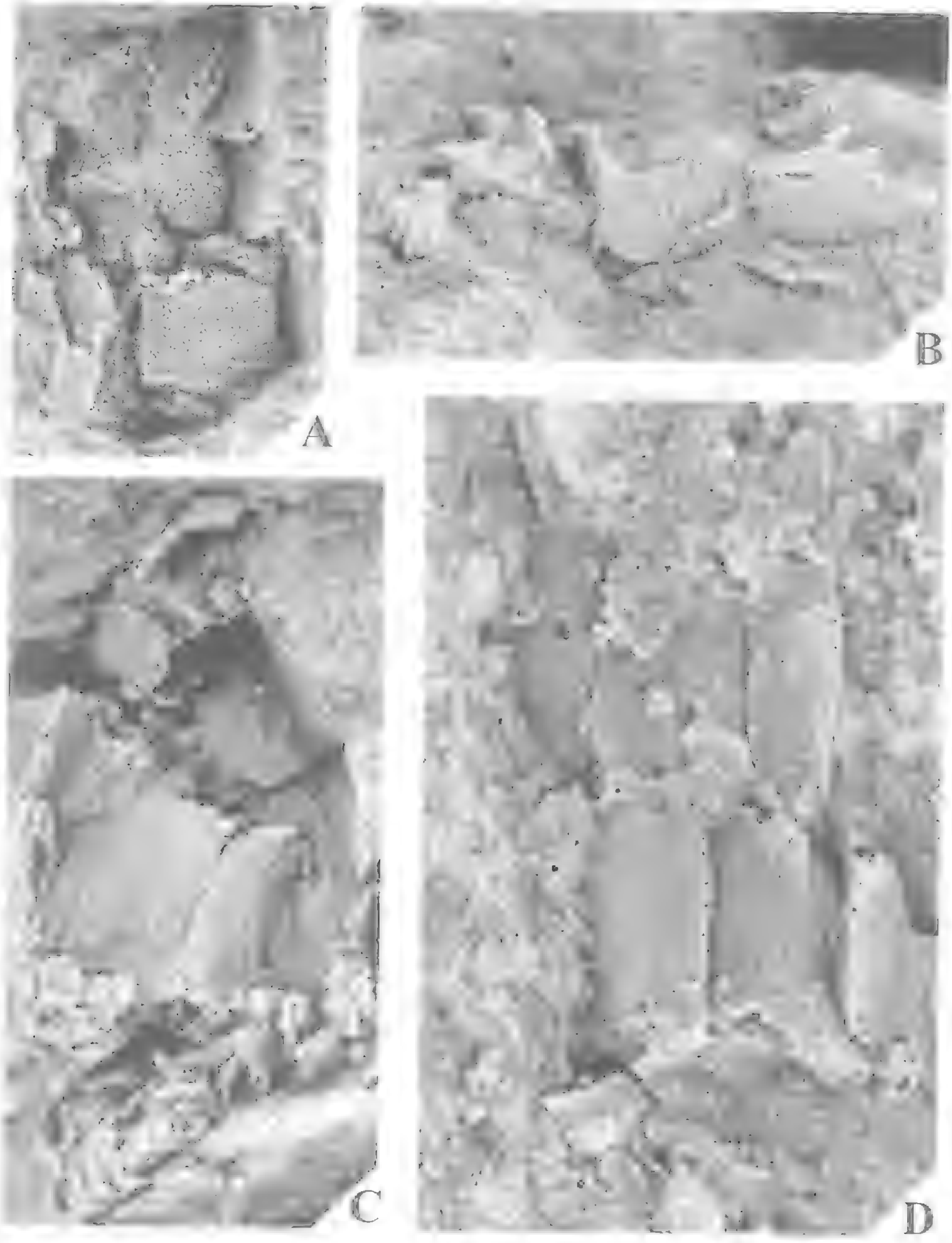


FIG. 10. *Protocytidium elliottae* gen. et sp. nov. A, partial convex surface. NMVP100435, ×7. B, lateral view of proximal appendage and plano-concave surface of NMVP100430, ×8. C, inside of plano-concave surface of NMVP100399, ×12. D, partial convex surface of NMVP100416, ×12.

in transverse section, with slightly raised proximal and distal margins, with straight central longitudinal furrow (sf in Fig. 12E) along proximal 2/3 of styloid, of uniform depth and width, shallowing to rounded proximal termination and distally in subelliptical pit (sp in Fig. 12E), with proximal margin slightly concave medially. Articular surface (Fig. 12E) with 4 irregular pits laterally on left and right.

*Distal part.* Largest observed number of ossicles 11 (Fig. 1D), articulated with paired plates. Ossicles only slightly higher than wide, triangular in cross-section (Fig. 10C), diminishing in size distally; lateral surfaces flat or gently convex in abapical 1/2, slightly depressed in apical 1/2; apical margin blunt, sloping distally, with blunt bulbous apex. Apex developed mainly on 3 or 4 most proximal ossicles, decreasing rapidly distally, absent on distal ossicles. Articular margins of ossicles along zig-zag line, divided into smaller, distal portion in contact with plate of next distal segment and larger, proximal part sutured with plate of corresponding segment. Plates subrectangular, partly overlapping each other proximo-distally. Articular margin of plates thicker proximally, gently tapering distally.

*Stereom.* Appendage externally with shallow irregular pits. Tetramerous rings and free margins of styloid blades sometimes coarsely granular. Radiating trabeculae on both styloid blades.

REMARKS. Material is often considerably disrupted and partly deformed. Very few specimens approach completeness, and the distal part of the convex surface is invariably damaged or missing. In some cases, the body plates are disarticulated but lie close to each other so that their mutual spatial relationships are almost unchanged. Preservation of the plano-concave surface is generally better than that of the convex surface, but the precise arrangement of the orifice plates can be deduced only by combining information from different individuals. In some specimens, both spines are visible and in the holotype, these are found in close proximity to the body, although only the left spine is preserved articulated with the toroidal projection on the distal surface of left DLM. The appendage is always incompletely preserved, although isolated ring plates of the proximal part, the abapical surface of the styloid and external ossicle morphology can be reconstructed.

Despite tectonic deformation, it is possible to distinguish 2 morphological variants. Homologous plates in individuals belonging to these variants show slightly different length/width ratios (e.g. PLM, ILM and DLM) and, sometimes, remarkably different shapes (e.g. A and C). The possibility that the 2 variants represent the effects of compression of the body along different directions cannot be entirely ruled out. Intraspecific and ontogenetic variation or sexual dimorphism could also be responsible. Similar problems were discussed by Ruta & Bartels (1998) in their analysis of tectonic deformation in *Rhenocystis latipedunculata* Dehm, 1932. Unlike *Rhenocystis*, specimens of *P. elliottae* have not been found in proximity to one another on the same slab surface and, therefore, retrodeformation techniques could not be applied to the Australian taxon. The first variant is more frequently represented with elongate, subelliptical to pyriform body outline and usually has markedly elongate plates A and C. In the second, rarer variant the body is only slightly longer than wide, subrectangular; both marginal and central plates of plano-concave surface are shorter; in particular, A and C are wider than long, subrhomboidal in outline and of equal width. The 2 variants do not seem to be related to body size, although some specimens belonging to the first category are among the largest known.

## ORIGIN AND EVOLUTION OF THE ALLANICYTIDIIDAE

Established by Caster & Gill (1967) to accommodate Early Devonian *Allanicytidium flemingi* from the Reefton Group of New Zealand, the Allanicytidiidae has expanded to now include 7 Southern Hemisphere anomalocystitids (*Allanicytidium*, *Notocarpos*, *Tasmanicytidium* and *Protocytidium* from Australia, *Placocystella* from South Africa and *Occultocystis* and *Australocystis* from South America). Philip (1981) recognised the almost identical plating pattern in *Allanicytidium* and *Notocarpos garratti* (Ludlow), although he did not note the lateral orifice plates in the latter taxon and misinterpreted the arrangement of C20 and C22 (Caster, 1983). Caster (1983) provided a diagnosis and revision of the allanicytidiids with his description of *Tasmanicytidium burretti* (Llandovery). Haude (1995) modified the diagnosis to include *Occultocystis koeneni* (Early Devonian). Prior to discovery of *Protocytidium*, *Occultocystis* provided the only link between Late Ordovician mitrate faunas from Laurentia and mid-Palaeozoic mitrates from Gondwana.

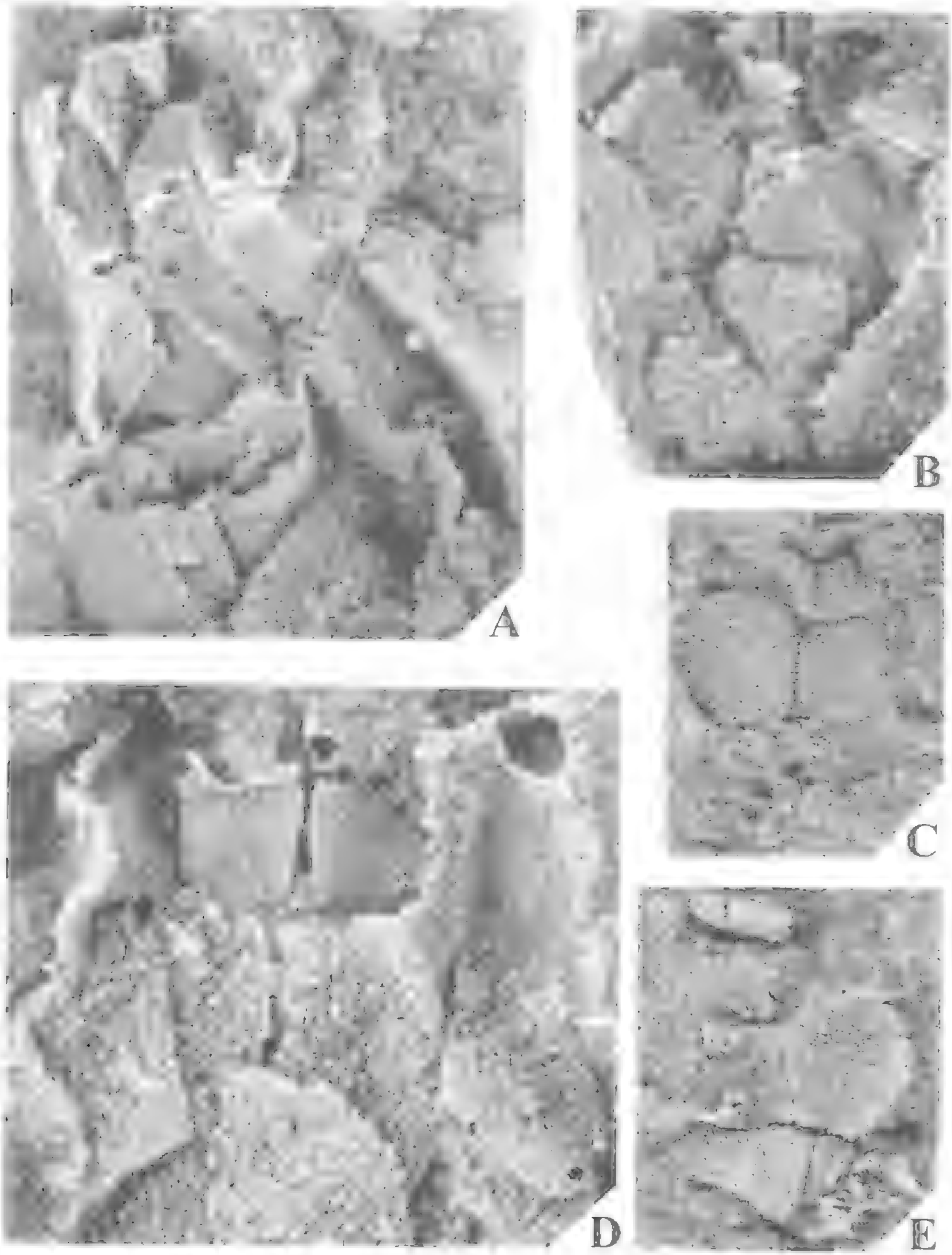


FIG. 11. *Protocytidium elliottae* gen. et sp. nov. Inside of plano-concave surface, convex surface, orifice plates and stereom. A, inside of plano-concave surface of NMVP100421, ×12. B, partial convex surface of NMVP100460, ×12. C, E, partial convex surface of NMVP100428, ×7. D, detail of distal part of Fig. 5C showing inside of orifice plates of NMVP100398, ×20.

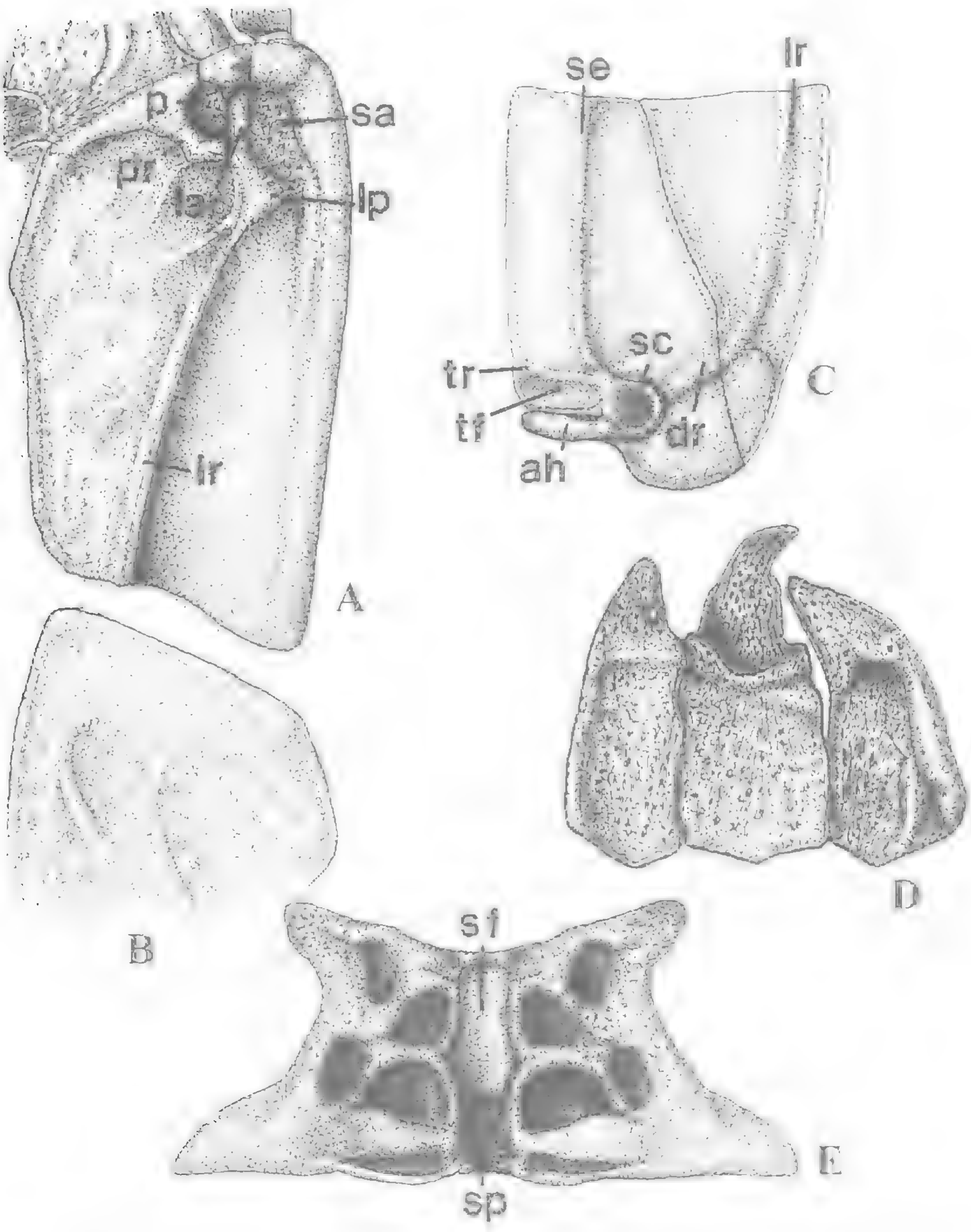


FIG. 12. *Protocytidium elliottae* gen. et sp. nov. Reconstruction of internal features of body. A, left DLM and left LOP, based on NMVP100401. B, right DLM based on NMVP100418. C, left PLM and left PM, based on NMVP100393. D, inside of MOP and LOP, reconstructed from NMVP100398, 100401, 100403 and 100488. E, abapical surface of styloid, based on NMVP100417. Abbreviations as in text. Drawings not to scale.

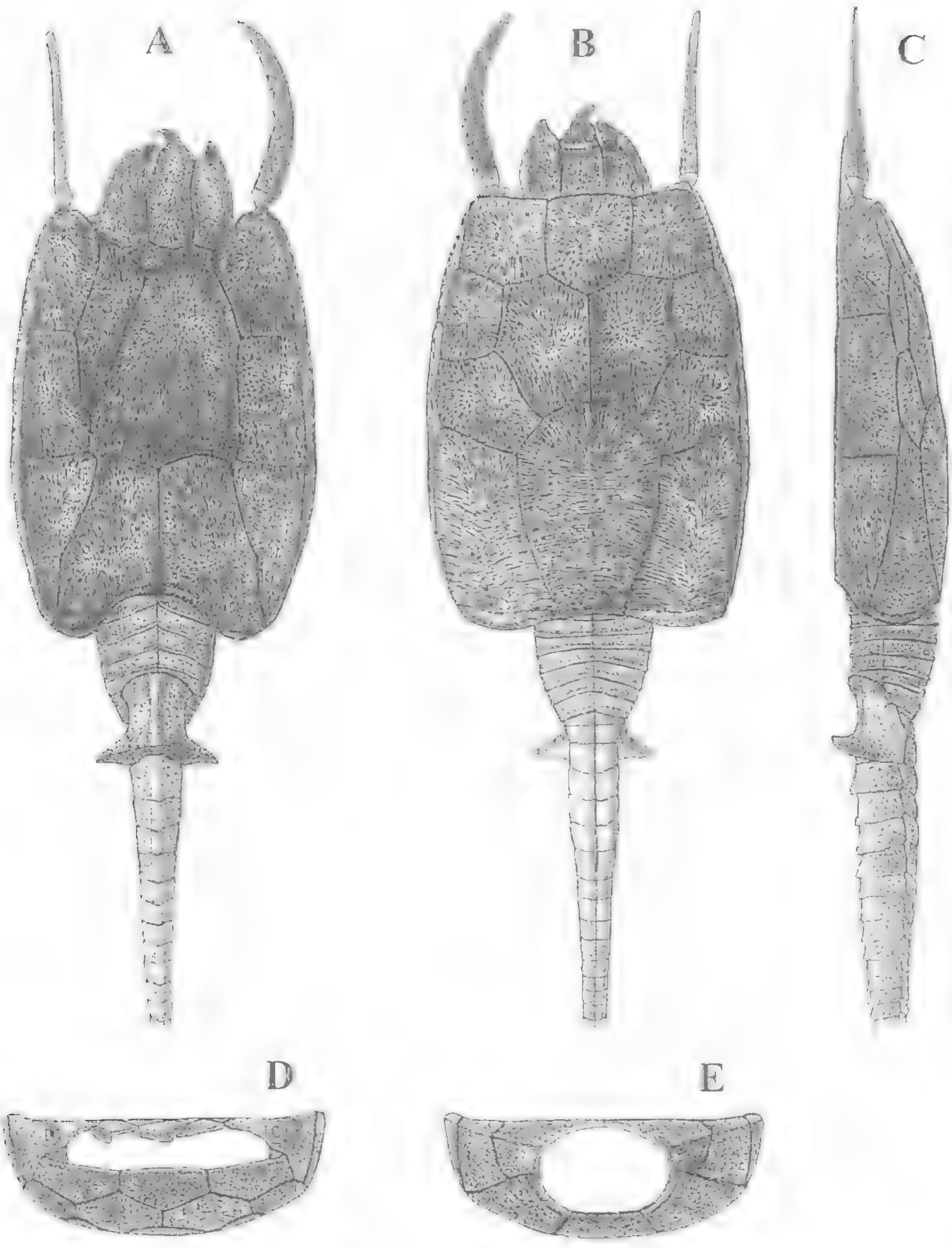


FIG. 13. Reconstruction of *Protocytidium elliottae* gen. et sp. nov. A, plano-concave surface. B, convex surface. C, right lateral view. D, proximal view (spines omitted). E, distal view (appendage omitted).

Character analysis of the allanicytidiids and relatives was undertaken by Ruta & Theron (1997). *Enoploura* is the sister-group to monophyletic Allanicytidiidae (Ruta in press). Ruta & Theron (1997) assigned *Placocystella africana* (Reed, 1925) and *Australocystis langei* Caster, 1956 (Early Devonian) to the Allanicytidiidae and recognised that the plano-concave surface of *Tasmanicytidium* is similar to that of more derived allanicytidiids (Caster, 1983; Ruta, in press).

*Mongolocarpos minzhini* Rozhnov, 1990 (Ludlow; Mongolia) is removed from the Allanicytidiidae despite the proximo-distal elongation of plate A. It is here considered a close relative of *Placocystites, Rhenocystis* and *Victoriacystis* following Ruta (in press).

## *ENOPLOURA* AND THE ORIGIN OF THE ALLANICYTIDIIDS.

*Enoploura popei* Caster, 1952 (Fig. 14A) has been described in great detail (Caster, 1952; Parsley, 1991). Its distalmost transverse row of plates on the convex surface has 5 elements as in *Barrandeocarpus norvegicus* Craske & Jefferies, 1989 and the anomalocystitids *Anomalocystites cornutus* Hall, 1858, *Bokkeveldia oosthuizeni* Ruta & Theron, 1997, *Mongolocarpos minzhini* Rozhnov, 1990, *Placocystites forbesianus* de Koninck, 1869, *Rhenocystis latipedunculata* Dehm, 1932 and *Victoriacystis wilkinsi* Gill & Caster, 1960. The lateral plates of the distalmost transverse row in *Enoploura* overlap the admedian plates as well as the marginal plates just proximal to them (Parsley, 1991). These marginal plates and the 2 large central plates lying medial to them may correspond to C6-C9 in *Bokkeveldia*, in which the admedian plates of row II, C7 and C8, are relatively large in comparison with other plates of the convex surface, as well as in other anomalocystitids. As an alternative hypothesis, the marginal plates sutured with C20 and C22 and the two large central plates of the convex surface of *Enoploura* may be homologous with the lateral (C15 and C19) and admedian (C16 and C18) plates of row IV in *Bokkeveldia*.

*Enoploura* and *Ateleocystites guttenbergensis* Kolata & Jollie, 1982 are similar in configuration of rows II and III in the latter resembling that of the 2 distalmost rows of *Enoploura*. Thus, *Enoploura* differs from *Ateleocystites* in possessing a shortened convex side (Parsley, 1991) in which the distal, 5- plated row would correspond to row II of *Ateleocystites*; the row proximal to it would be homologous to row III of *Ateleocystites* and the 2 marginal elements in contact with C20 and C21 on the right side and with C21 and C22 on the left side would correspond to the lateral elements of row IV (C15 and C19) in *Ateleocystites*. Furthermore, the proximo-distal imbrication pattern of the 2 large central plates of *Enoploura* is similar to that of the admedian elements of row III (C11 and C13) in *Ateleocystites*.

According to Parsley (1991), the body of *Enoploura* is progenetically shortened in comparison with that of other mitrates. This is an intriguing hypothesis, but it needs to be corroborated by additional fossil evidence. A derivation of *Enoploura* from taxa with a polyplated convex surface is likely, but not certain. Despite its specialised features (e.g. morphology of the styloid; plate arrangement of the convex surface), *Enoploura* retains a primitive skeletal configuration on the plano-concave surface, as indicated by plate B. Such a configuration suggests that this genus probably evolved from an ancestor resembling such Laurentian genera as *Ateleocystites* (Ruta, in press).

*PROTOCYTIDIUM*: BASAL ALLANICYTIDIID. Skeletal configuration of *Protocytidium elliottae* (Fig. 14B) invites comparisons with *Enoploura* and with such basal allanicytidiids as *Occultocystis*. Affinities of *Protocytidium* with the allanicytidiids are suggested by the central plates of the plano-concave surface, especially the proximo-distally elongate plate A, and by the longitudinal styloid keel, a semicircular, proximal styloid blade and a proximally recumbent distal blade. The distal 2/3 of C21 is similar in shape and proportions to its homologue in *Tasmanicytidium*.

However, although plate A is more elongate and narrower than in *Notocarpos* and is shaped like its homologue in such allanicytidiids as *Placocystella*, it does not contact left PLM as in all allanicytidiids more derived than *Notocarpos* (Caster, 1956, 1983; Caster & Gill, 1967; Ruta & Theron, 1997; Ruta & Jell, 1999c; Ruta, in press). Although MOP is longer than LOP, it is not as expanded transversely as in *Notocarpos, Tasmanicytidium, Placocystella, Allanicytidium* and *Australocystis*. Furthermore, both LOP plates are wider proximally than distally and not wedged obliquely between MOP and DLM (MOP and LOP not known in detail in *Occultocystis*).

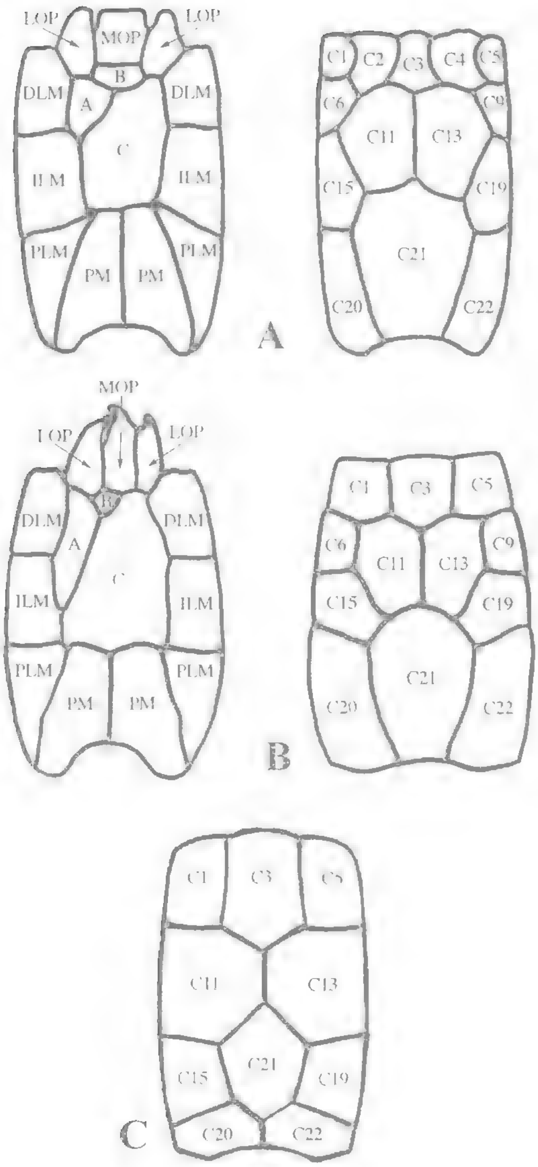


FIG. 14. Plano-concave (left) and convex (right) surfaces of A, *Enoploura popei* (redrawn and modified from Parsley, 1991). B, the basal allanicytidiid *Protocytidium elliottae*. C, convex surface of *Occultocystis koeneni* (redrawn and modified from Haude, 1995). Drawings not to scale.

Except for the occurrence of 3 (as in *Occultocystis*) rather than 5 distal plates, skeletal configuration of the convex surface of *Protocytidium* differs from that of *Enoploura* mainly in the relative size and proportion of various plates. The 3 distalmost plates of the convex surface (especially C3) are larger in *Protocytidium* than in *Enoploura* but smaller than in *Occultocystis*. Both in *Enoploura* and in *Protocytidium* LOP and MOP project distal to the body orifice and are divided into proximal and distal parts ('thecal' and 'lip' of Parsley, 1991). Gaps are present distally between MOP and LOP but they are smaller and more irregular than in *Enoploura*. The transverse thickening on the internal surface of LOP and MOP is another similarity between *Protocytidium* and *Enoploura*. More striking resemblances are on the internal side of the plano-concave surface, especially in the asymmetrical development of internal ridges near the latero- distal angles of the left and right DLM.

Plate B, generally regarded as a primitive character for the anomalocystitids (Craske & Jefferies, 1989; Ruta & Theron, 1997; Ruta, in press), is much smaller in *Protocytidium* than in *Enoploura* and other mitrates and appears to be displaced slightly to the left of the longitudinal body axis. Furthermore, B does not contact right LOP and is strongly asymmetrical in outline. C6, C9, C15 and C19 of *Enoploura* differ from their homologues in *Protocytidium* in being much longer than wide. Relative size and proportions of C11, C13 and C21 are similar in both taxa.

The coarsely pitted to labyrinthine stereom in *Enoploura popei* (Caster, 1952; Parsley, 1991) is only vaguely reminiscent of the external skeletal texture of *Protocytidium*. The latter appears to be less coarse, presumably as a result of the much smaller body size of *Protocytidium*, and more variable both on the surface of single body plates and on different plates. Resemblances between the body stereom of *Enoploura* and that of *Protocytidium* nevertheless occur in the vermicular to ridge-like pattern of C20 and C22 and the lateral body walls.

TRANSITIONAL *OCCULTOCYSTIS*. In *Occultocystis* (Fig. 14C), C21 is not as large as in other allanicytidiids and is not interposed between C20 and C22. On both right and left of its convex surface, a plate may occur which is perhaps incompletely fused with C20 and C22 respectively (Haude, 1995). The distal margin of the convex surface consists of 3 plates, of which the median one is narrow and elongate with concave lateral margins as in *Enoploura*. It is likely that the marginal plates sutured along the midline of the convex surface of *Occultocystis* are homologous with the 2 large central elements of *Enoploura*.

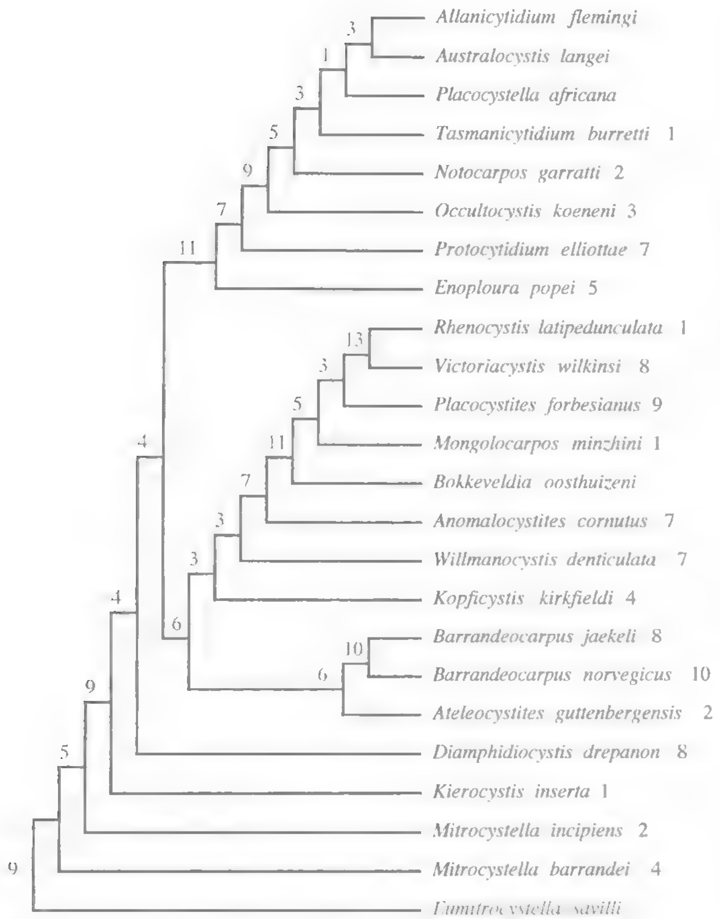


FIG. 15. Most parsimonius tree resulting from cladistic analysis. Numbers indicate branch lengths.

Plating of the convex side of *Occultocystis* differs from that of other allanicytidiids in several details. The transition from this genus to more derived allanicytidiids was probably characterised by the disappearance of the median element of the distalmost transverse row and by elongation of C21 both distally and proximally.

The evolutionary history of more derived allanicytidiids is characterised by remarkably few character changes, most of which pertain to general proportions and relative size of plates of convex surface, skeletal sculpture and appendage morphology (Ruta & Theron, 1997; Ruta & Jell, 1999c; Ruta, in press).

## PHYLOGENETIC ANALYSIS

Data from a study of interrelationships of the anomalocystitid mitrates (Ruta, in press) are used here to establish the phylogenetic position of *Protocytidium elliottae*. Morphological characters are those discussed by Ruta (in press) with coding for *Kierocystis inserta* Parsley, 1991 accounting for the reconstruction of the proximal 1/3 of the convex surface proposed by Parsley (1991; pers. comm., 1997). Some characters of the spines are entered as polymorphic for *Protocytidium*. The matrix includes 24 taxa and 106 binary characters and was analysed with PAUP Version 3.1.1 on a Power Macintosh 7500/100 using the same heuristic search settings as detailed by Ruta (in press).

The analysis yielded a single tree (length = 230 steps; consistency index excluding uninformative characters = 0.456; retention index = 0.68; rescaled consistency index = 0.322) (Fig. 15). Major differences between this tree and the 3 equally parsimonious solutions found by Ruta (in press) are: 1) *Barrandeocarpus jaekeli* Ubaghs, 1979 and *B. norvegicus* Craske & Jefferies, 1989 are sister taxa and, together, form the sister-group of *Ateleocystites guttenbergensis* Kolata & Jollie, 1982; 2) *Kierocystis inserta* Parsley, 1991 and *Diamphidiocystis drepanon* Kolata & Guensburg, 1979 are successively more closely related to the remaining ingroup taxa.

*Protocytidium* occupies an intermediate position between *Enoploura popei* Caster, 1952 and the Allanicytidiidae as defined by Haude (1995) and Ruta (in press), thus confirming the transitional nature of several of its features. The following characters, all showing state change 0-1 numbered in the same order as they appear in the data matrix (Ruta in press) and accompanied by their consistency index (ci) values, support the sister-group relationship between *Protocytidium* and the Allanicytidiidae under the accelerated character-state transformation (character changes are placed as close to the root of the tree as possible, thus emphasising reversals): 21 (ci=1), plate MOP longer than each of the 2 plates LOP; 30 (ci=0.333), spine length greater than

length of distal margin of plano-concave surface; 87 (ci=0.25), 3 plates along distalmost margin of convex surface; 90 (ci=1), interior of distal margin of convex surface with transverse thickening with asymmetrical cross-section; 97 (ci=1), distal styloid blade inclined proximally; 99 (ci=0.25), a sharp, longitudinal keel on external surface of styloid; 102 (ci=1), proximal styloid blade semicircular in outline. With the exception of characters 30, 87 and 99, the other characters are uniquely derived features of the clade (*Protocytidium elliottae* + remaining Allanicytidiidae). When the delayed character-state transformation is used (character changes are placed as far from the root of the tree as possible, thus emphasising parallelisms), the clade comprising *Protocytidium elliottae* and the remaining Allanicytidiidae is supported by state changes relative to characters 21, 30, 97, 102 as well as by character 53 (ci=0.25), absence of overlapping elements on convex surface. From this pattern of character distribution, it is possible to highlight the major changes during allanicytidiid evolution.

Modifications of the plano-concave surface include: reduction in size and subsequent loss of B; proximo-distal elongation of A and subsequent interposition of it between C and left lateral marginal DLM, ILM and PLM; narrowing and acquisition of oblique orientation of right and left LOP, which became wedged between MOP and right and left DLM, respectively; widening of MOP; acquisition of flexible articulation between orifice plates and adjacent plates of plano-concave surface.

Modifications of the convex surface include: reduction of distal row of plates from 5 to 3 to 2 elements; great expansion of C21; arrangement of marginal plates in 4 sets of paired elements surrounding C21; projection of most distal pair of plates beyond distal margins of LOP and MOP.

Modifications of the appendage include: reduction in number of tetramerous rings; acquisition of semicircular outline of free margin of proximal styloid blade; proximally recumbent position of distal styloid blade; lateral ear-like projections of distal blade.

## CONCLUSIONS

The diverse mitrate fauna of Australasia is enriched by addition of the latest Ordovician anomalocystitid *Protocytidium elliottae*. Spine morphology, external stereom texture and skeletal configuration of body plates distinguish this mitrate from other anomalocystitids. Character analysis indicates that *Protocytidium* is the most primitive member of the Allanicytidiidae. Character distribution patterns and comparison of this genus with *Enoploura* and *Occultocystis* suggest several skeletal modifications in evolution of the allanicytidiids including: 1) simplification of the convex surface plating through loss of plates; 2) modification of the orifice plates to form a flexibly articulated structure; 3) increase in the degree of bilateral symmetry of the body; 4) loss of plate B; 5) proximo-distal elongation of plate A; and 6) lateral expansions of distal styloid blade.

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## LITERATURE CITED

CASTER, K.E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology 34: 1-47.

1956. A Devonian placocystoid echinoderm from Paraná, Brazil. Paleontologia do Paraná (Centennial Volume): 137-148.

1983. A new Silurian carpoid echinoderm from Tasmania and a revision of the Allanicytidiidae. Alcheringa 7: 321-335.

CASTER, K.E. & GILL, E.D. 1967. Family Allanicytidiidae, new family. Pp. S561-S564. In: Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York).

CRASKE, A.J. & JEFFERIES, R.P.S. 1989. A new mitrate from the Upper Ordovician of Norway, and a new approach to subdividing a plesion. Palaeontology 32: 69-99.

DEHM, R. 1932. Cystoideen aus dem rheinischen Unterdevons. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie. Beilage-Band, Abteilung A 9: 63-93.

GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology 41: 5-71.

HALL, J. 1858. Scientific intelligence, II, geology, 4. Crinoids of New York. American Journal of Science and Arts 25: 277-279.

HAUDE, R. 1995. Echinodermen aus dem Unter-Devon der argentinischen Präkordillere. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 197: 37-86.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3: 1-128.

KOLATA, D.R. & GUENSBURG, T.E. 1979. *Diamphidiocystis*, a new mitrate carpoid from the Cincinnatian (Upper Ordovician) Maquoketa Group in southern Illinois. Journal of Paleontology 53: 1121-1135.

KOLATA, D.R. & JOLLIE, M. 1982. Anomalocystitid mitrates (Stylophora, Echinodermata) from the Champlainian (Middle Ordovician) Guttenberg Formation of the Upper Mississippi Valley Region. Journal of Paleontology 56: 531-565.

KONINCK, M.L. de. 1869. Sur quelques Echinodermes remarquables des terrains paléozoiques. Bulletin de l'Academie Royale des Sciences Belgique 28: 544-552.

PARSLEY, R.L. 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). Bulletins of American Paleontology 100: 5-57.

PHILIP, G.M. 1981. *Notocarpos garratti* gen. et sp. nov., a new Silurian mitrate carpoid from Victoria. Alcheringa 5: 29-38.

REED, F.R.C. 1925. Revision of the fauna of the Bokkeveld beds. Annals of the South African Museum 22: 27-226.

ROZHNOV, S.V. 1990. New representatives of the class Stylophora (Echinodermata). Paleontological Journal 24: 34-45.

RUTA, M. in press. A cladistic analysis of the anomalocystitid mitrates. The Zoological Journal of the Linnean Society.

RUTA, M. & BARTELS, C. 1998. A redescription of the anomalocystitid mitrate *Rhenocystis latipedunculata* from the Lower Devonian of Germany. Palaeontology 41: 771-806.

RUTA, M. & JELL, P. A. 1999a. *Adoketocarpus* gen. nov., a mitrate from the Ludlovian Kilmore Siltstone and Lochkovian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 377-398.

1999b. Two new anomalocystitid mitrates from the Lower Devonian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 399-422.

1999c. Revision of Silurian and Devonian Allanicytidiidae (Anomalocystitida, Mitrata) from southeastern Australia, Tasmania and New Zealand. Memoirs of the Queensland Museum 43: 431-451.

RUTA, M. & THERON, J.N. 1997. Two Devonian mitrates from South Africa. Palaeontology 40: 201-243.

UBAGHS, G. 1967. Stylophora. Pp. S496-S565. In: Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York).

1979. Trois Mitrata (Echinodermata: Stylophora) nouveaux de l'Ordovicien de Tchécoslovaquie. Paläontologische Zeitschrift 53: 98-119.

VANDENBERG, A.H.M. 1992. Kilmore 1:50,000 map and geological report. Geological Survey of Victoria Report 91: 1-86, + map.

VANDENBERG, A.H.M., RICKARDS, R.B. & HOLLOWAY, D.J. 1984. The Ordovician-Silurian boundary at Darraweit Guim, central Victoria. Alcheringa 8: 1-22.

WETHERBY, A.G. 1879. Description of a new family and genus of Lower Silurian Crustacea. Journal of the Cincinnati Society of Natural History 1: 162-166.

## APPENDIX

Through this and the following 4 papers by the same authors reference is made to a system of plate nomenclature proposed in a paper by the senior author that remains in press with The Zoological Journal of the Linnean Society of London (Ruta, in press). To facilitate the use of this nomenclature in the papers published in this volume a key to that plate notation is provided below.

Plating of the convex surface is shown on the lefthand diagram and of the plano-concave surface on the right. The convex surface is based on the maximum regular plating known which occurs in the South African *Bokkeveldia oosthuizeni* Ruta & Theron, 1997. This terminology has been developed to avoid entirely any implied interpretation of orientation or function and although no thanks may be forthcoming for introducing another terminology in an already contentious area we believe use of terminology which removes all interpretation is desirable and should be of benefit to the enduring arguments surrounding these animals.

The following abbreviations are employed on the figure:- On the convex surface 'c' prefix is for convex and equates to the 'v' for ventral used by Ruta & Theron (1997).

On the plano-concave surface

PM = proximal marginal plates

PLM= proximal lateral marginal plates

ILM= intermediate lateral marginal plates

DLM = distal lateral marginal plates

LOP = lateral orifice plates

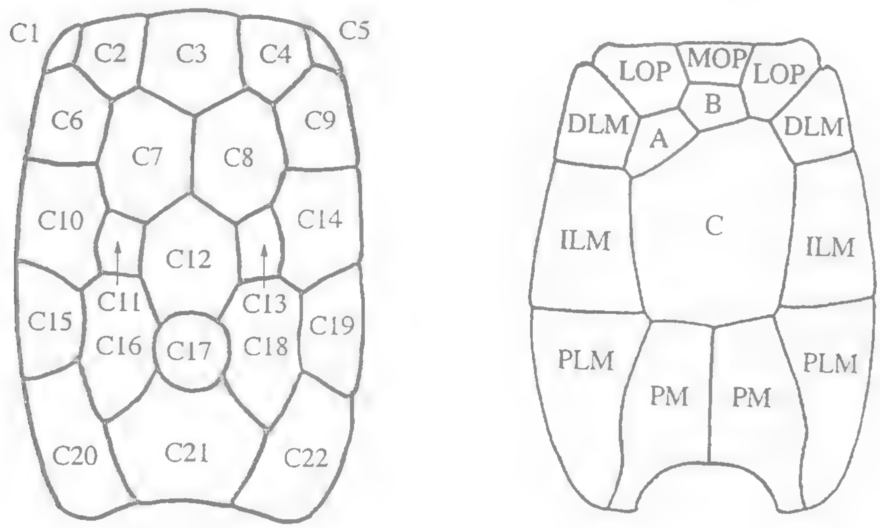
MOP = median orifice plate

Central plates:-

A = anomalocystid plate

B = second asymmetrical plate of some genera

C = largest central plate



# *ADOKETOCARPUS* GEN. NOV., A MITRATE FROM THE LUDLOVIAN KILMORE SILTSTONE AND LOCHKOVIAN HUMEVALE FORMATION OF CENTRAL VICTORIA

MARCELLO RUTA AND PETER A. JELL

Ruta, M. & Jell, P.A. 1999 06 30: *Adoketocarpus* gen. nov., a mitrate from the Ludlovian Kilmore Siltstone and Lochkovian Humevale Formation of central Victoria. *Memoirs of the Queensland Museum* **43**(1): 377-398. Brisbane. ISSN 0079-8835.

The mitrate *Adoketocarpus* gen nov. is the first representative of the Paranacystidae from Australia. It occurs in central Victoria with *A. acheronticus* sp. nov. in the Ludlovian Kilmore Siltstone and *A. janeae* sp. nov. in the Lochkovian part of the Humevale Formation. *Adoketocarpus* has a simplified plate arrangement on the convex surface and a strongly twisted orifice; plating of the plano-concave surface resembles that of Middle Ordovician *Eumitrocystella savilli* from Morocco suggesting that the paranacystids may derive from boreal mitrocystitids. Fewer lateral marginal plates of the plano-concave surface, loss and size reduction of distal plates and enlargement of proximalmost plates of the convex surface would attend evolutionary transition from boreal mitrocystitids to paranacystids. Paranacystids formed a clade whose origin and evolution were apparently in Gondwanaland, where they probably dispersed in the Ordovician/Silurian. ❒ *Paranacystidae, Adoketocarpus, Silurian, Devonian, Victoria.*

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The known Australian carpoid fauna of 4 endemic genera with 6 species is more abundant than faunas from other parts of Gondwana. Some Australian carpoids have affinities with species from Europe and North America (Gill & Caster, 1960; Ruta, 1997a), whereas others have affinities with taxa from South America, South Africa and New Zealand (Caster, 1956, 1983; Caster & Gill, 1967; Philip, 1981; Haude, 1995; Ruta & Theron, 1997). The new genus described herein has its nearest relatives in the Lower Devonian of South America and South Africa.

Among Australian carpoids none are closely related to the new genus. *Rutroclypeus* is the only solute known from Australia; it occurs in the Lower Devonian of Kinglake, Victoria, with *R. junori* (Withers, 1933), *R. victoriae* Gill & Caster, 1960 and *R. ? withersi* Gill & Caster, 1960. The other 3 monotypic genera are mitrate stylophorans of the Anomalocystitida: *Tasmanicytidium burretti* Caster, 1983 from the upper Llandovery Richea Shale of SW Tasmania, *Notocarpos garratti* Philip, 1981 from the upper Ludlovian part of the Humevale Formation near Whittlesea, central Victoria and *Victoriacystis wilkinsi* Gill & Caster, 1960 (Ruta, 1997a) from the lower Ludlovian in the Dargile Formation near Heathcote and the Melbourne Formation at Hawthorn.

Extensive collections of echinoderms from the mid-Palaeozoic of central Victoria made over many years, but mainly during the early 1980s, are housed in the Museum of Victoria. This paper deals with a new paranacystid mitrate genus from the Upper Silurian and Lower Devonian of central Victoria. It is important because: 1, it is the first Australian record for the Paranacystidae Caster, 1954; 2, its occurrence in the Upper Silurian is the earliest for the family, predating the Lower Devonian record in South America (Caster, 1954; Haude, 1995); 3, its anatomy can be reconstructed in detail, thus throwing light on several poorly known aspects of the paranacystids and prompting a new interpretation of their skeleton (Caster, 1954; Ruta, 1997c). 4, it provides additional evidence of the affinities between Siluro-Devonian mitrate faunas of Australia and the Malvinokaffric Realm (Caster, 1954, 1956, 1983; Gill & Caster, 1960; Caster & Gill, 1967; Philip, 1981; Parsley, 1991; Haude, 1995; Ruta & Theron, 1997; Ruta, 1997c).

LOCALITIES. The mitrates described in this work are from 4 different localities in the Museum of Victoria locality register (NMVPL) representing 3 horizons.

NMVPL252 Middendorp's Quarry at Kinglake West is marked on the map of Williams (1964) and discussed elsewhere (Ruta & Jell, 1999); it

occurs in the Humevale Formation and the brachiopod fauna indicates the *Boucotia janeae* Brachiopod Zone (Garratt, 1983) of mid Lochkovian age.

NMVPL1924 (=T95 of Williams (1964)) is in fine sandstones in the bed of Mathieson Creek, 2km S of the Kinglake West to Flowerdale Road. Carpoids are a minor component of an extensive fauna dominated by diverse crinoids and stelleroids and including brachiopods, bryozoans, corals (*Pleurodictyum* only), bivalves and several other minor groups. Williams (1964) showed this site to be in the same Sandstone Member (probably the Flowerdale Sandstone Member) as Collins Quarry near Kinglake West which is Lochkovian (Vandenberg, 1988) based on the brachiopods (Garratt, 1983).

NMVPL1927 is on the eastern bank of Broadhurst Creek, where it crosses the Kilmore to Wandong Road, SSW of Kilmore in central Victoria. The locality occurs at 37°20'30"S, 144°59'35"E (Grid Reference 220652) on the Kilmore 1:50,000 Geological Map (Vandenberg,1992). The fossils come from the Kilmore Siltstone (Vandenberg,1992), a sequence of predominantly thin (5-10cm), horizontally banded siltstones and very thin (less than 1cm), cross-bedded sandstones with rare, irregularly interbedded turbidite sandstones. The sequence is more than 3,500m thick. This huge thickness of siltstone indicates very rapid deposition on a tectonically stable shelf.

Graptolites indicate an early Ludlow age (Vandenberg,1992) for the upper Kilmore Siltstone in the Kilmore district, from which most of the shelly faunas have been collected. Trilobites predominate, with rare brachiopods, bryozoans, ostracodes and rugose corals, all of which are concentrated mainly in coarse sandstones. Echinoderms are locally abundant in thick sandstone beds (Vandenberg, 1992). NMVPL 1927 occurs lower in the sequence and is most probably early Ludlow in age, although the possibility that it belongs to the late Wenlock cannot be ruled out.

NMVPL1960 refers to material excavated from a pipeline trench about 2km towards Kilmore along the Kilmore to Wandong Road from NMVPL1927 in similar lithology and horizon.

## SYSTEMATIC PALAEONTOLOGY

A standard anatomical nomenclature for mitrates does not exist (Caster, 1952; Caster & Gill, 1967; Ubaghs, 1967; Kolata & Jollie, 1982; Jefferies, 1986; Cripps, 1990; Kolata et al., 1991; Parsley, 1991, Beisswenger, 1994; Ruta, 1997a, b; Ruta & Theron, 1997). The terminology of Ruta (in press) is followed for the external skeleton and plating pattern except that, for brevity, 'left' and 'right' replace 'anomalocystid' and 'abanomalocystid' respectively. For the internal anatomy, we use Ubaghs' (1967, 1969) nomenclature, although reference is necessary to some other sources (Jefferies, 1986; Jefferies, 1973; Jefferies & Lewis, 1978; Cripps, 1990; Beisswenger, 1994; Ruta & Theron, 1997).

Unless otherwise stated illustrations are of latex casts from decalcified siltstone, whitened with ammonium chloride sublimate.

Class STYLOPHORA Gill & Caster, 1960
Order MITRATA Jaekel, 1918
Suborder incertae sedis
Family PARANACYSTIDAE Caster, 1954

DIAGNOSIS (modified from Caster, 1954 and Ruta, 1997c). Plates A and C proximo-distally elongate, markedly different in shape and size; C separated from left DLM and left PLM by A. Left PM slightly larger than right PM, with chevron-shaped distal margin. Lateral and proximal marginal plates with well-developed subvertical projections. Skeletal sculpture of small elliptical knobs or tooth-like serrations along lateral margins of PLM plates, sometimes extending on proximal parts of lateral margins of left DLM and right EXM/ILM. Proximal 1/2-2/3 of convex body surface formed by proximo-distally elongate, shield-like C20 and C22. Distal part of convex surface of 2 smaller, subtrapezoidal plates with sinuous to gently concave lateral and distal margins and pronounced latero-distal angles. Small, subquadrangular to lozenge-shaped plate, possibly homologous with C21, between C20 and C22, proximally and subtrapezoidal plates, distally. Proximal part of appendage shorter than maximum width of each PM plate. Styloid with slightly expanded to flared, non-recumbent blades and proximal stout articulation process. Proximal ossicles of distal part of appendage expanded transversely and much more robust than successive ossicles.

### **Adoketocarpus** gen. nov.

TYPE SPECIES. *Adoketocarpus acheronticus* sp. nov.

ETYMOLOGY. Greek *adoketos*, unexpected and *carpos*, a fruit; refers to body shape and unusual skeletal features. Masculine.

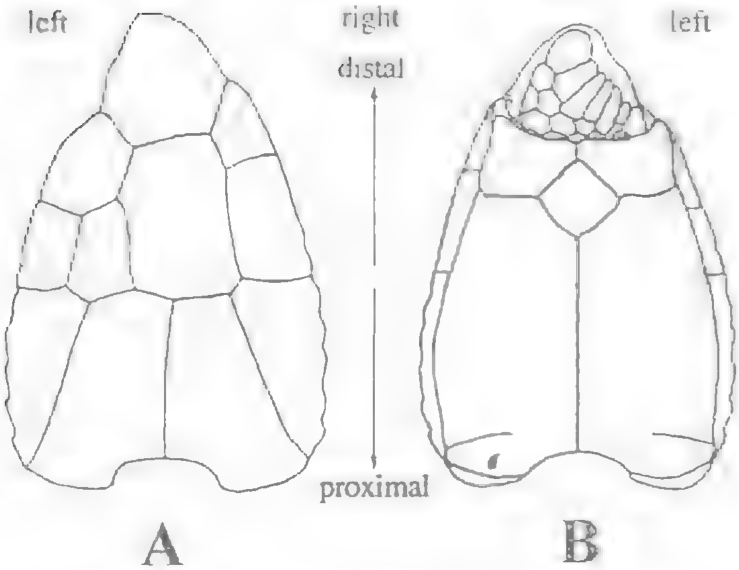


FIG. 1. Orientation of the skeleton of *Adoketocarpus acheronticus* gen. et sp. nov. A, plano-concave surface. B, convex surface.

DIAGNOSIS. C at least twice as wide as A. Length of left and right PLM exceeding that of other lateral marginal plates. Lateral serrations on PLM plates decreasing in size proximo-distally, sometimes extending on proximal part of lateral margins of left DLM and right EXM/ILM. Maximum width of proximal part of appendage less than maximum width of proximal margin of each PM plate.

**Adoketocarpus acheronticus** sp. nov.
(Figs 1-2, 3D, 4-10, 11A,D,E, 12A-D)

ETYMOLOGY. Greek *Acheron*, a river of the underworld in Greek mythology; most specimens were collected on the bank of a stream.

MATERIAL. Holotype: NMVP100330. Paratypes: NMVP100331-100348 from NMVPL1927. Other material: NMVP100349-100356, QMF37202, 37208, 37212, 37213, 37214 from NMVPL1927; NMVP149357-149358 from NMVPL1960.

DIAGNOSIS. Lateral body margins gently convex. Plate A subpentagonal to wedge-shaped, slightly to much wider proximally than distally and c. 1/2 as large as C. Right LOP slightly smaller than C, roofing over the body orifice, with almost straight proximo-lateral margins and sinuous latero-distal margins; distal process pronounced, with blunt, rounded end. Left DLM much shorter than right EXM/ILM, about as long as and slightly narrower than left LOP. Left LOP larger than right DLM, contributing to distal 1/3 of left lateral body margin. Subvertical projections of left and right PM straight to gently convex externally; suture between left and right PM bending slightly rightward distally. Plate C about as wide proximally as distally, with chevron-shaped proximal margin. Suture between A and C sinuous, gently concave rightward proximally, more deeply concave leftward distally. Suture between distal subtrapezoidal plates of convex surface shorter than their proximal and proximo-medial margins.

DESCRIPTION. EXTERNAL. Body longer than wide, ovato-lanceolate to pyriform, slightly (Figs 1-2, 3D, 4A-E, 5C, 11A,B,D). Maximum width about twice as far away from distal process of right LOP as from proximal excavation for appendage insertion. Lateral margins more strongly convex proximally than distally; right margin slightly longer than left margin. Subvertical projections of lateral marginal plates visible when the convex surface is oriented towards the observer (Figs 4F, 6A,C,D, 7A,B, 11E, 12D). Distal body orifice twisted leftward and framed by radially arranged platelets of different shape and size (Figs 4F, 6A-D). Plano-concave surface slightly raised along lateral margins and near proximo-lateral angles and shallower centrally (Figs 4A-E, 5A-D). Maximum curvature of convex surface at the level of its proximal 1/3 (Figs 6A, C, 7B, 9B).

*Measurements*. Holotype (Fig. 4A): c.4.7mm wide and 6.7mm long. Smallest specimen (Fig. 4C,F): c.2.7mm wide and 3.7mm long. Largest specimen (Fig. 4E): estimated body width and length c.5.7mm and 7.7mm, respectively.

*Plano-concave surface*. Weakly concave surface of 11 medium to large plates. Marginal plates in 2 groups of 3, a distal element roofing over the body orifice and 2 proximal elements contributing to excavation for appendage insertion (Figs 1A, 2A, 3D, 4A-E, 5A,C, 11A,B,D). Height of subvertical projections of lateral marginal plates approximately constant over most of their length,

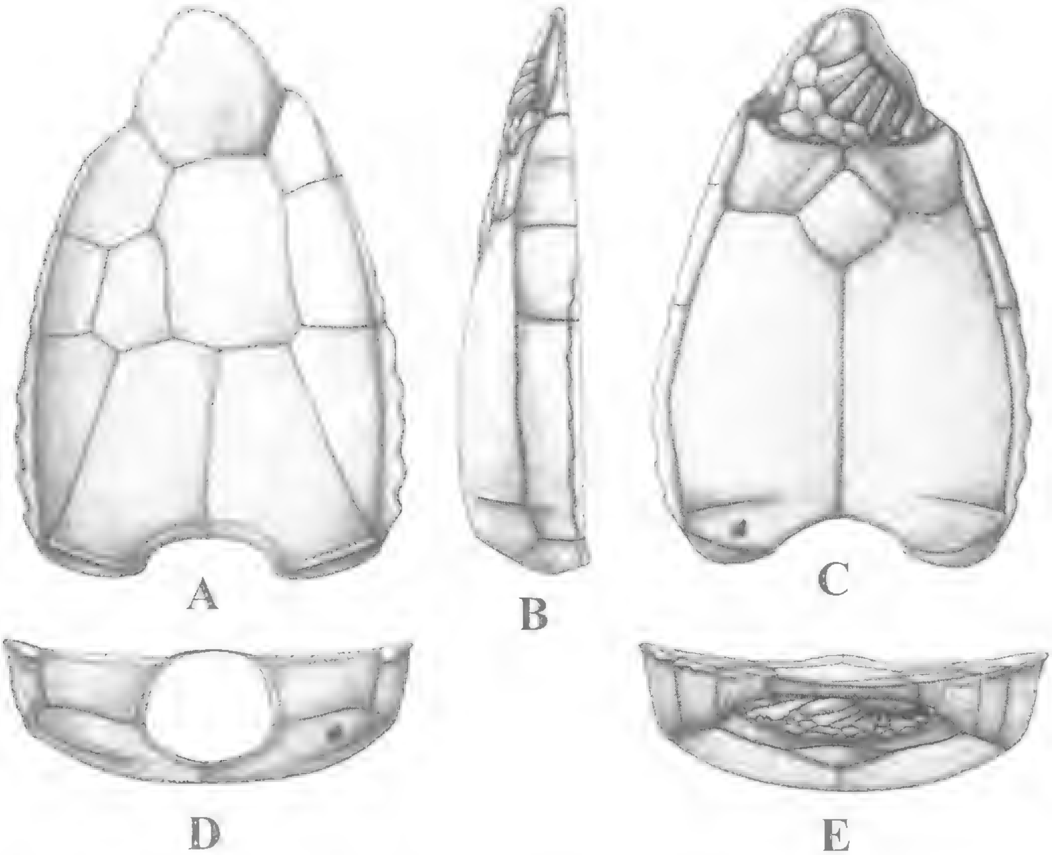


FIG. 2. Reconstruction of *Adoketocarpus acheronticus* gen. et sp. nov. (appendage omitted). A, plano-concave surface; B, left lateral view. C, convex surface. D, proximal view. E, distal view (hatched area shows space possibly occupied in life by polygonal plates).

only slightly decreasing near latero-distal angles of plano-concave surface and at the level of proximal 1/3 of both left and right PLM (Figs 2B, 4D-E, 5A,C, 6A,C, 7A, 11E); subvertical projections of PM plates higher than those of lateral marginal plates, rectangular to trapezoidal in proximal view and flat to gently convex externally (Figs 2A-D, 4D, 5A-D). Subpentagonal left LOP and trapezoidal right DLM forming latero-distal angles of plano-concave surface; left LOP slightly wider and longer than right DLM. Left DLM and right EXM/ILM subrectangular and proximo-distally elongate; length of left DLM c.2/3 that of right EXM/ILM. Left and right PLM subequal in shape and size, triangular and contributing to proximo-lateral angles of body; lateral margins of both plates PLM with 4-5 serrations rapidly decreasing in size proximo-distally and either gradually merging into each other or neatly separated; 2-3 proximalmost serrations with blunt, rounded apex, steep distal margin and gentle proximal margin; 1-2 very shallow serrations near proximal 1/3 of lateral margins of left DLM and right EXM/ILM (Figs 1A, 2A, 3D, 4A-D, 5C, 7A, 11A). Distal margin of left PM longer than distal margin of right PM and chevron-shaped, the right arm of the chevron being as long as or longer than its left arm; median 1/2 of proximal margins of both plates PM excavated for insertion of appendage; suture between such plates generally bending slightly rightward distally; transverse thickening sometimes observed along their proximal margins (Figs 4D-E, 5A-D). Irregularly pentagonal right LOP slightly smaller than C, with prominent plectrum-shaped to semicircular distal process, gently sinuous latero-distal margins and almost straight proximo-lateral margins (Figs 4A-E, 5A,C, 11A,B,D); distal process immediately left of longitudinal body axis. Plate A

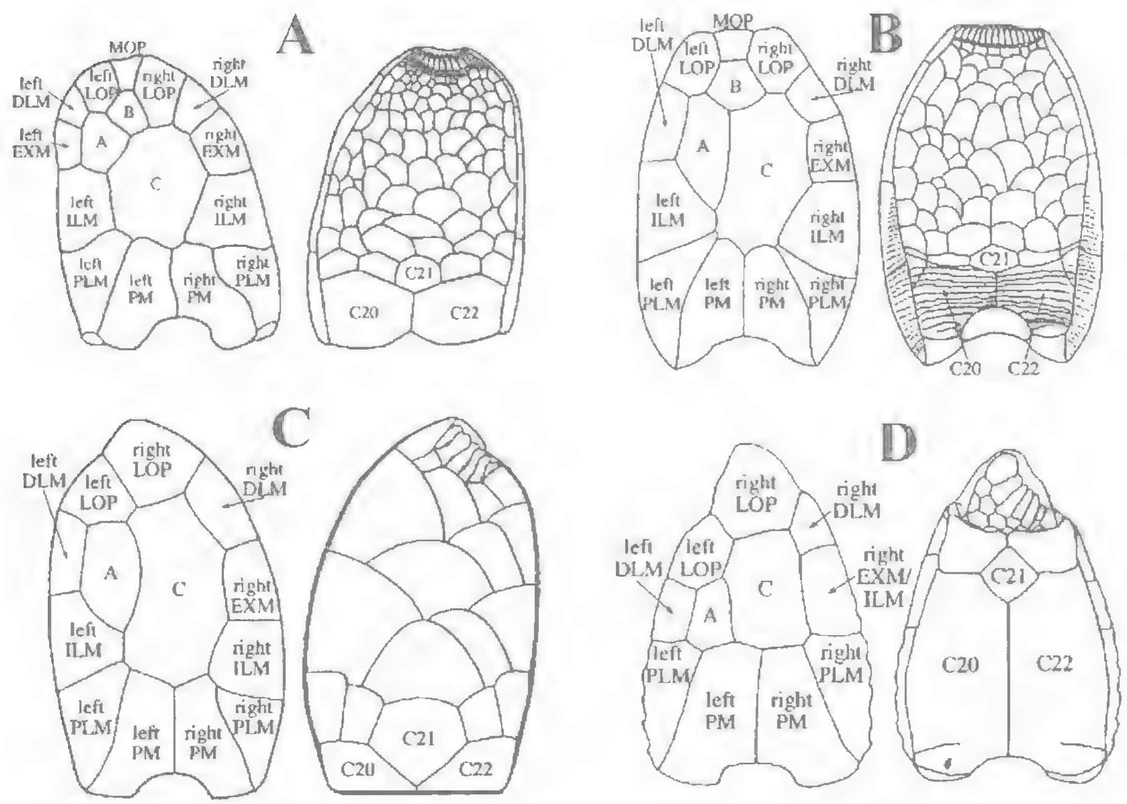


FIG. 3. Plate nomenclature of the plano-concave (left) and convex (right) surfaces in 3 mitrocystitids and in *Adoketocarpus acheronticus* gen. et sp. nov. Specimens not to the same scale. A, *Mitrocystella barrandei* (redrawn from Ubaghs, 1968). B, *Mitrocystella incipiens* (simplified from Jefferies, 1986). C, *Eumitrocystella savilli* (modified from Beisswenger, 1994). D, *Adoketocarpus acheronticus* gen. et sp. nov.

subpentagonal to wedge-shaped, longer than wide, slightly to much wider proximally than distally, comparable in size with left and right DLM (Figs 4A-D, 5C, 11A,B,D) and in contact with left LOP latero-distally, left DLM laterally, left PLM proximo-laterally and left PM proximo-medially. C twice as long and wide as A and in contact with right LOP distally, right DLM latero-distally, right EXM/ILM laterally, right PLM proximo- laterally and right and left PM proximally (Figs 2A, 3D). Suture between A and C with deep leftward concavity distally and less pronounced rightward concavity proximally (Figs 4A-D).

*Convex surface*. Convex surface of 5 small to large plates symmetrically arranged in centre, plus 8 plates extending up lateral and proximal margins from plano-concave surface. Proximal 2/3 of convex surface of large, proximo-distally elongate, shield-like C20 and C22 plates, 1.5-2 times longer than wide (Figs 1B, 2C, 3D, 4F, 6A,C, 7B, 9A-C, 12B,D). Lateral 1/2 of proximal margins of such plates straight to strongly convex; median 1/2 deeply excavated for appendage insertion; lateral margins of both plates gently to moderately convex, sometimes showing abrupt curvature about half-way along their length; lateral and proximal margins merging into each other smoothly or at c.120° (Figs 4F, 6A,C-D, 7B,8B-D, 9A-C, 11C,E). Proximo-lateral part of external surface of both C20 and C22 distinctly sloping, almost vertical with respect to the rest of the plate in its distal 1/2 and delimited distally by straight, slightly pronounced keel with steeper distal and gentler proximal slope (Figs 2B-D, 6C, 7B, 9B-C). Keels running latero-medially and proximo-distally from proximo-lateral angles of both C20 and C22, their length being less than 1/2 the width of these plates. External margin of small facet for articulation with plates PLM visible on both C20 and C22 just latero-distal to lateral end of each keel (Figs 1B, 2B-D, 4F, 6A, C, 7B, 9B). Sub-elliptical to teardrop-shaped pit proximal to

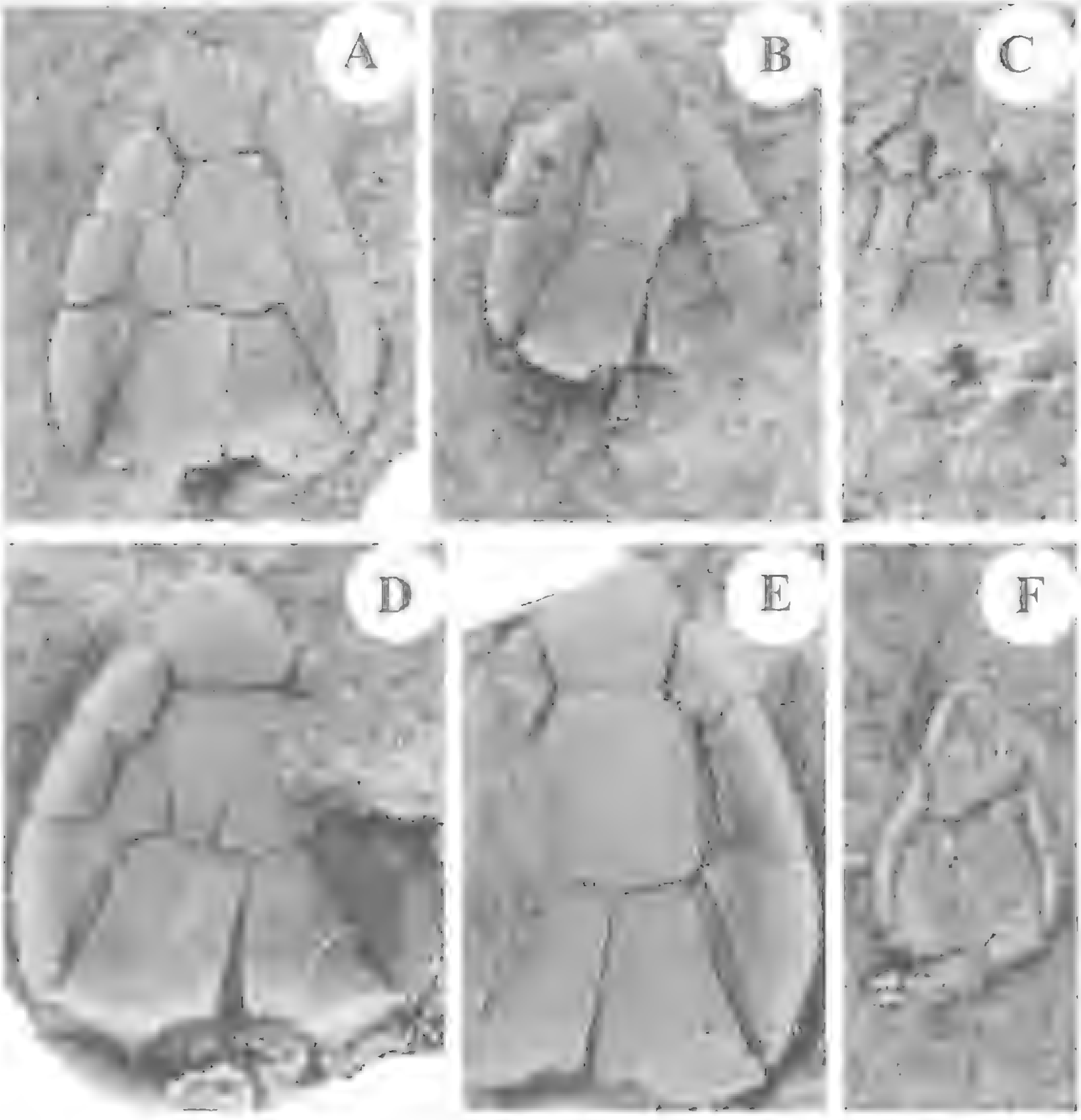


FIG. 4. *Adoketocarpus acheronticus* gen. et sp. nov., all from NMVPL1927, x10. A-E, plano-concave surface. F, convex surface. B, D, F, showing part of the appendage. A, NMVP100330, holotype. B, NMVP100331. C, F, NMVP100332. D, NMVP100333. E, NMVP100334.

median 1/3 of keel on C20 (Figs 1B, 2B-D, 6C, 7B, 9B). Distal 1/3 of convex surface occupied by 2 subtrapezoidal plates, slightly wider than long and in contact with each other along very short, straight suture and with C20 and C22 along gently sinuous sutures; latero-distal angles of subtrapezoidal plates with distally directed, blunt-ended processes (Figs 1B, 2B-C,E, 3D, 4F, 6A-D, 9B). Subquadrangular to lozenge-shaped C21 with straight to slightly convex margins in contact with medio-distal margins of C20 and C22 and with medio-proximal margins of subtrapezoidal plates (Figs 2B-C,E, 6A-D, 7B, 9B).

*Distal orifice*. Body orifice strongly twisted leftward, roofed over by right LOP and floored by 6-7 platelets arranged radially (Figs 1B, 2B-C, E, 4F, 6A-D). Right platelet subelliptical, with major axis almost perpendicular to longitudinal body axis; remaining platelets subrectangular to spike-shaped and decreasing progressively in

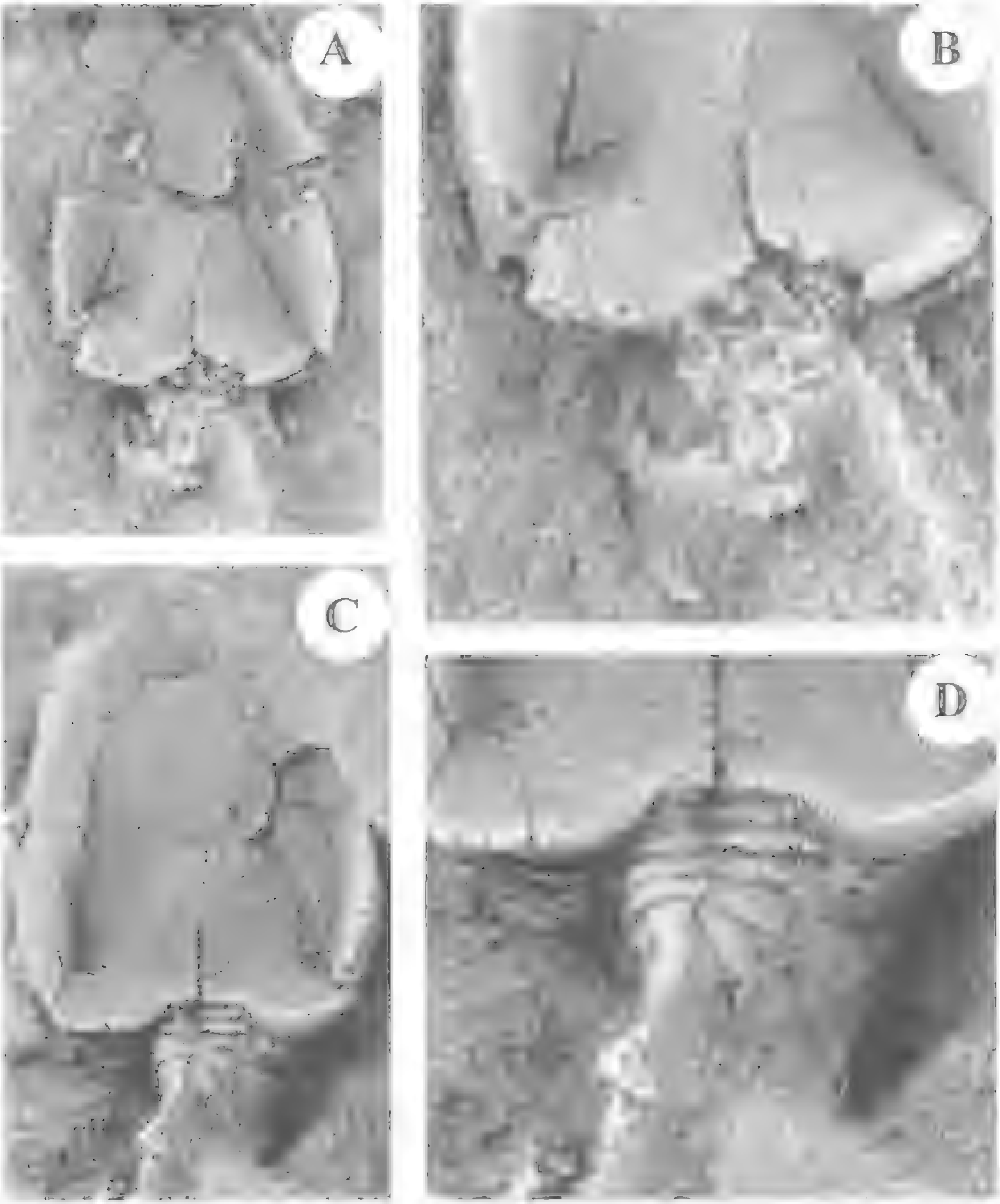


FIG. 5. *Adoketocarpus acheronticus* gen. et sp. nov., all from NMVPL1927. A,C, plano-concave surface. B,D, proximal part of appendage and styloid. A,B, NMVP100335, ×10 and ×20, respectively. C,D, NMVP100336, ×10 and ×20, respectively.

size from right to left; left platelet subtriangular, with major axis parallel to longitudinal body axis. Polygonal elements of irregular shape inserted between proximal margins of orifice platelets and distal margins of subtrapezoidal plates, more numerous on the right than on the left, smaller

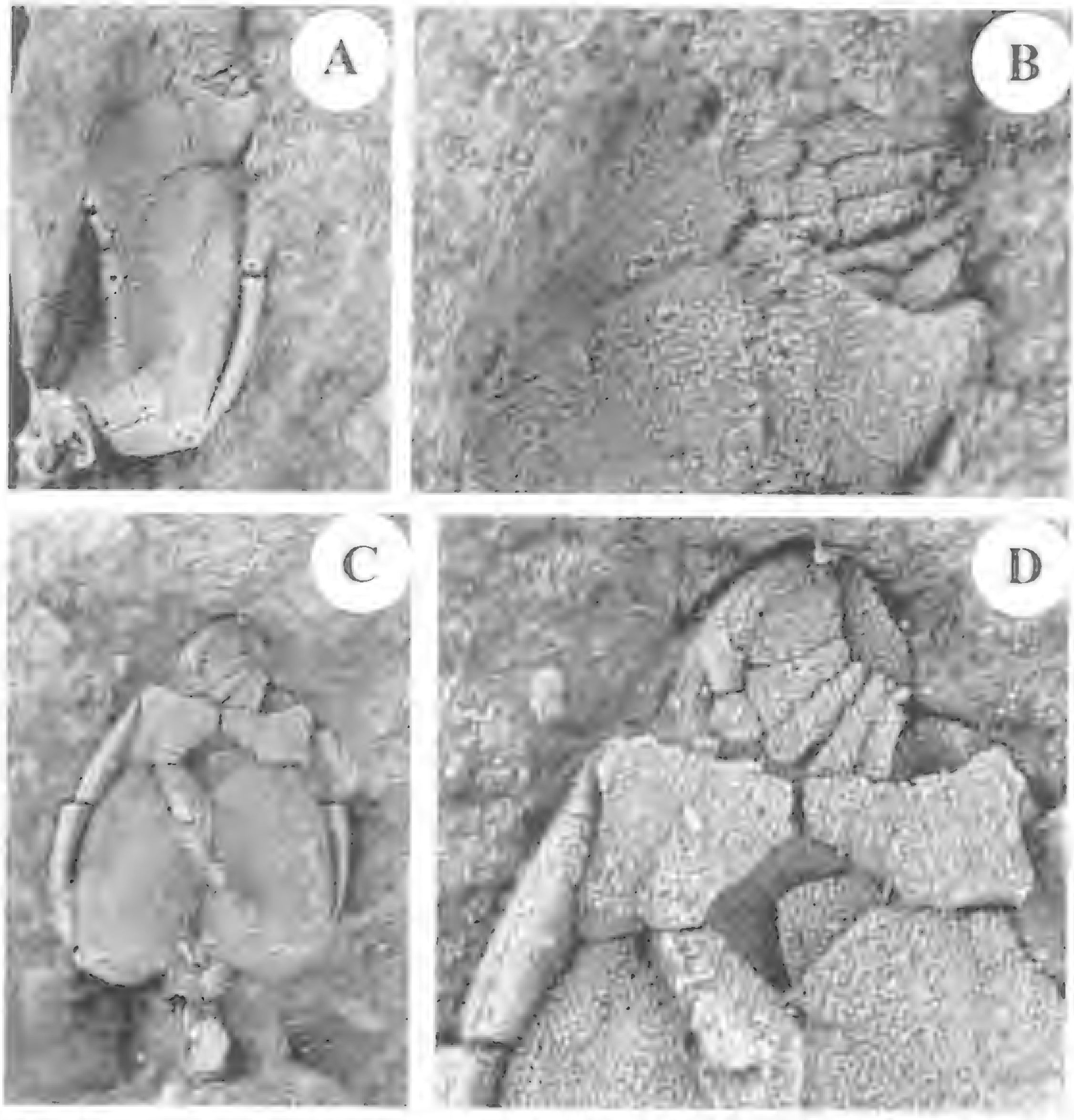


FIG. 6. *[illegible]* gen. et sp. nov., all from NMVPL1927. A,C, convex surface and proximal part of appendage. B,D, close-ups of orifice platelets. A,B, NMVP100337, ×10 and ×30, respectively. C,D, NMVP100338, ×10 and ×25, respectively.

and transversely elongate near distal margins of subtrapezoidal plates, larger near proximal margins of orifice platelets; polygonal elements probably also covering proximal part of right latero-distal margin of right LOP (Fig. 6C-D).

*Stereom.* Plates of plano-concave surface with irregular, highly variable external texture, ma consisting of subcircular to subelliptical pores separated by trabeculae (Figs 4A-E, 5A-C). Thinner trabeculae and smaller subcircular pores visible near lateral body margins. Trabeculae often forming a fringe near plate sutures, where the pores are narrow and elongate and arranged radially. Irregularly radiating pattern of sinuous, elongate, bifurcating trabeculae on marginal and subcentral plates, especially near their centres; adjacent trabeculae often sending at irregular intervals shorter, transverse trabeculae delimiting subrectangular to subelliptical pores.

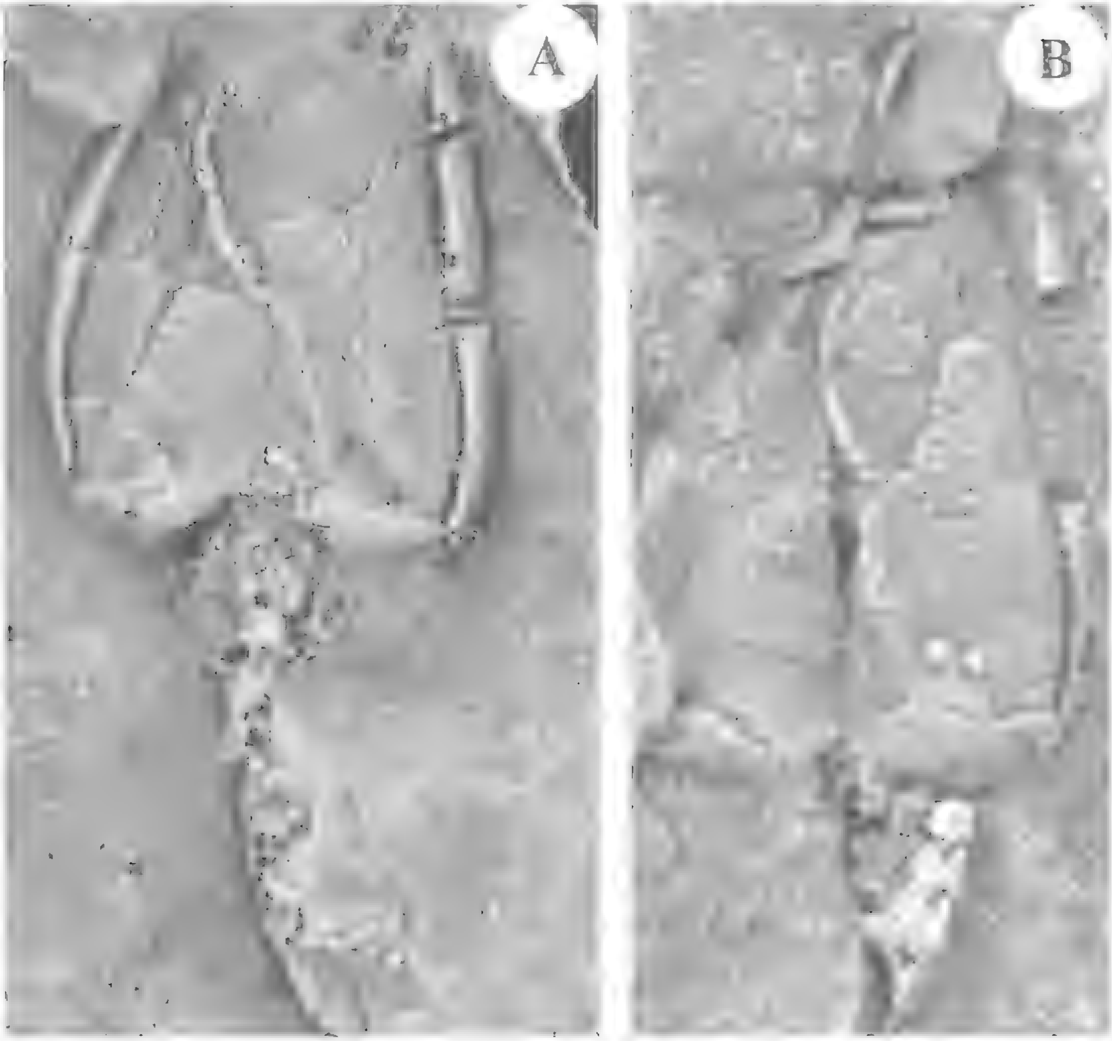


FIG. 7. *Adoketocarpus acheronticus* gen. et sp. nov., all from NMVPL1927. A, NMVP100339, inside of plano-concave surface and partially preserved appendage, ×10. B, NMVP100340, partially preserved convex surface, distal 1/3 of inside of plano-concave surface and disrupted appendage, ×15.

Stereom of subvertical projections of lateral marginal plates generally compact or consisting of minute subcircular pores. Stereom of convex surface almost uniformly composed of circular pores and short trabeculae, the latter arranged radially near the plate sutures (Figs 4F, 6A-D, 7B, 9B-C). Stereom of orifice platelets coarsely granular or with very shallow pits surrounded by weak ridges (Figs 4F, 6B,D).

INTERNAL. Plate C, right LOP (in part) and left and right PM reveal most of the inside of the plano-concave surface, but little is known about the interior of the lateral marginal elements (Figs 7A, 9B-C). So far as the convex surface is concerned, only the internal aspect of C20 and C22 is known in detail, whereas the inside of the distal 1/3 of this surface is only partially preserved.

*Plano-concave surface*. Right latero-distal angle of internal surface of right LOP occupied by median 1/3 of subcircular depression straddling suture with right DLM and continuing on adjacent part of internal surface of latero-distal angle of this plate (Figs 1B, 2C, E, 6C-D). Internal side of plano- concave surface divided into 2 fields by oblique septum (Ubaghs, 1967) (= oblique ridge of Jefferies, 1986) (Figs 7A-B, 8A; se in Fig. 10B); distal 1/3 of septum with marked

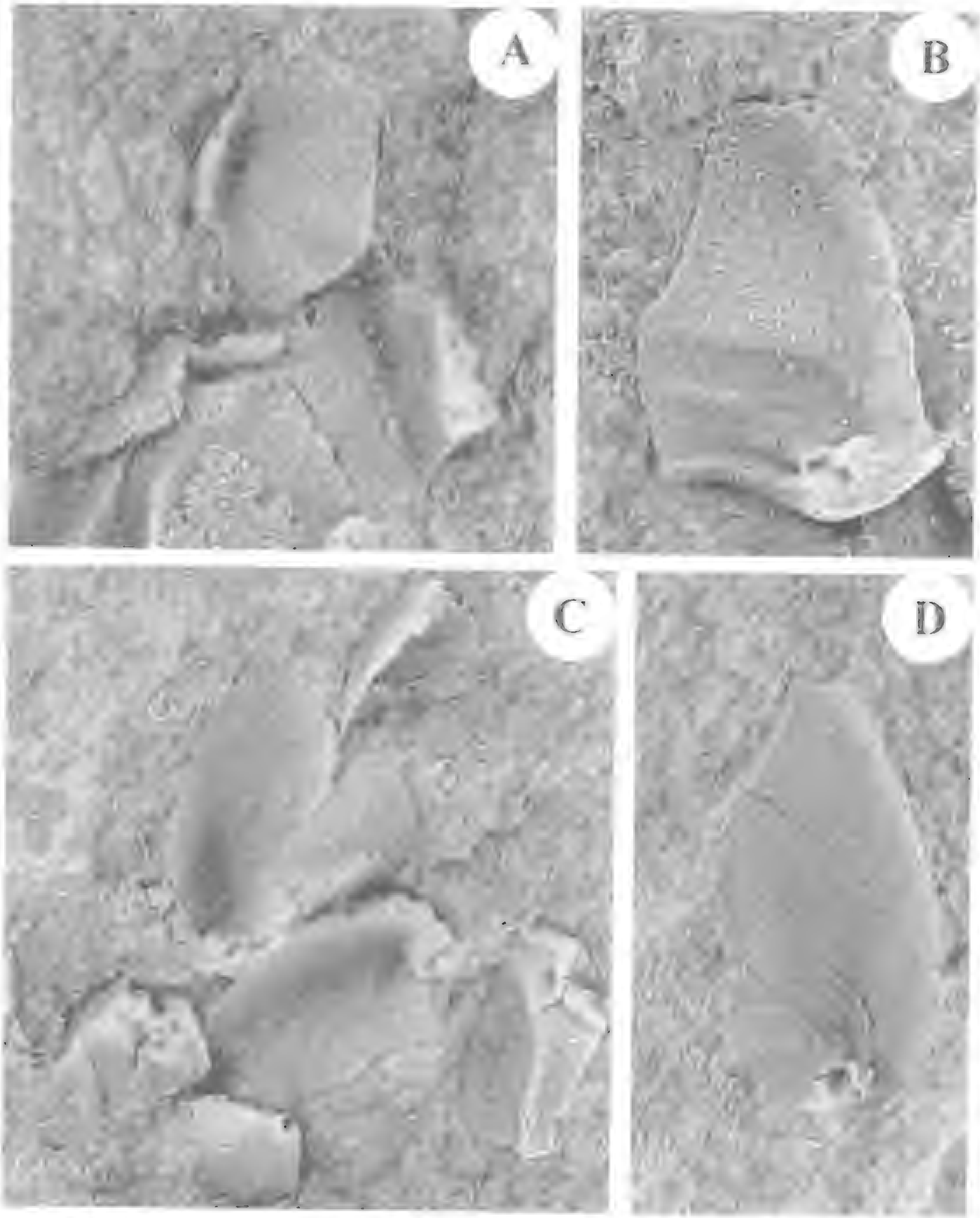


FIG. 8. *Adoketocarpus acheronticus* gen. et sp. nov., all from NMVPL1927. Internals of skeletal plates. A, NMVP100340, disrupted distal 1/3 of plano-concave surface, the element near top centre is right LO?, ×25. B, NMVP100342, inside of C20, ×20. C, NMVP100343, plates C20, C21, C22, left and right PM, left PLM, ×16. D, NMVP100344, inside of C20, ×12.

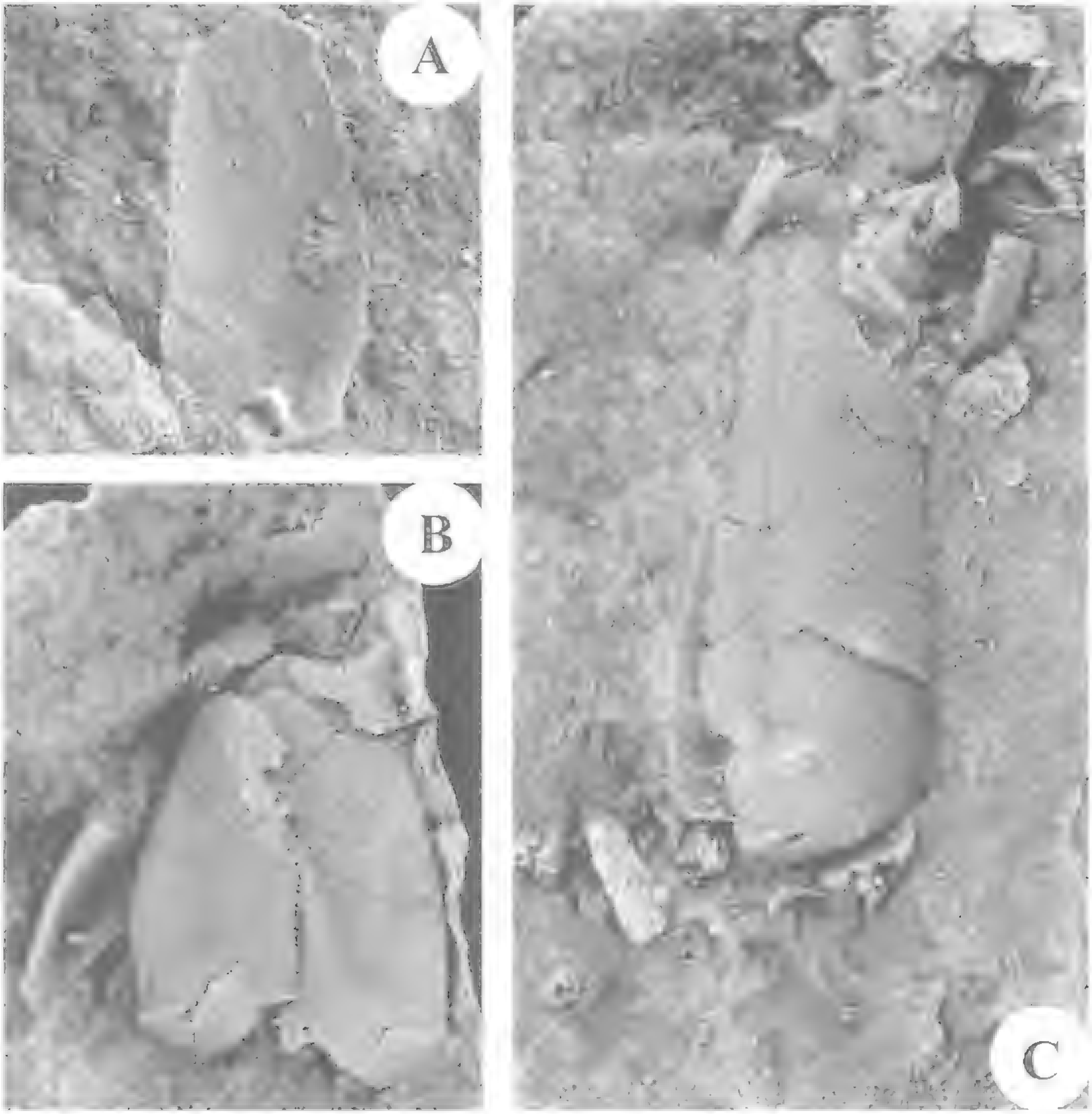

FIG. 9. *Adoketocarpus acheronticus* gen. et sp. nov., all from NMVPL1927. A, NMVP100345, inside of C20, ×12. B, NMVP100346, convex surface, partially disrupted distal 1/3, ×10. C, NMVP100347, slightly damaged C20 in external view, ×12.

rightward convexity occupying distal 2/3 of internal surface of C (Figs 6C-D, 7A-B, 8A); distalmost end rapidly weakening where it straddles suture between C and right LOP and vanishing distally on the internal surface of the latter; proximal 2/3 of septum straight, thicker than convex part and bending slightly to the right in cross-section; convex part passing gradually into straight part; boundary between these 2 parts delimited by elongate and poorly defined thickening (= diminutive spur of Ubaghs, 1967 and base of middorsal process of Jefferies, 1986) (Fig. 7A-B); straight part of septum running obliquely from internal side of proximal 1/3 of C to internal side of left PM, straddling suture just lateral to medio-distal angle of left PM (Fig. 10A-B).

Proximalmost end of septum merging into cup-like left scutula (Ubaghs, 1967) (= dorsal calcitic cup of left pyriform body of Jefferies, 1986) (sc in Fig. 10B) delimited by slightly raised, thick, subcircular scutular rim. Deep transverse furrow

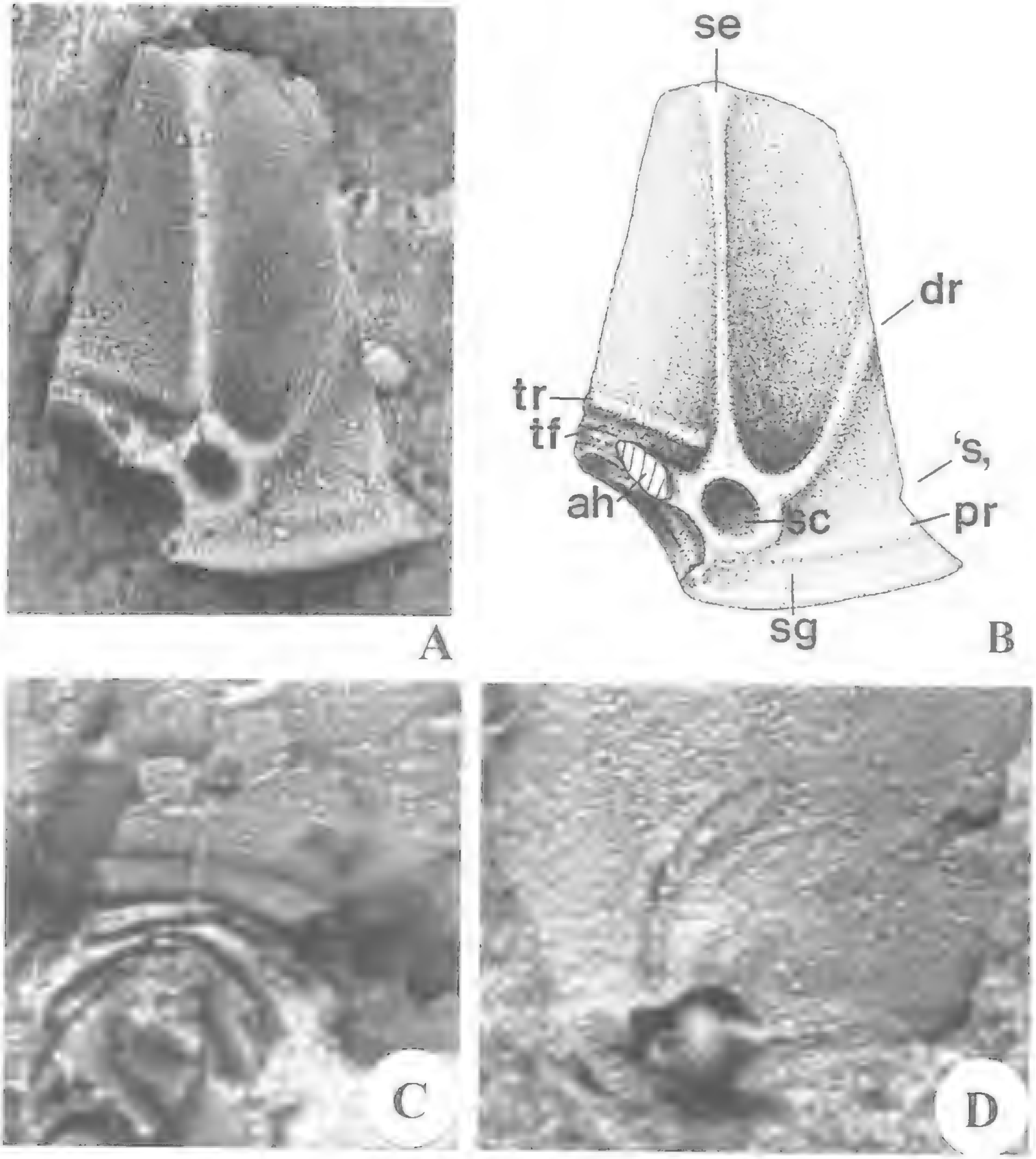


FIG. 10. *Adoketocarpus acheronticus* gen. et sp. nov., from NMVPL1927, internal surface of left PM plate. A, NMVP100348, ×25, latex cast coated with ammonium chloride. B, camera lucida drawing of the same specimen abbreviations as in text. C, NMVP100339, natural internal mould of proximal 1/3 of the 2 PM plates, ×25. D, NMVP100344, natural internal mould of proximal 1/3 of C20, ×25.

(= transverse anterior groove of Ubaghs, 1967 and anterior boundary of posterior coelom of Jefferies, 1986) (tf in Fig. 10B) running from medio-distal part of scutular rim to median margin of both left and right PM and delimited distally by prominent transverse ridge, straight to slightly convex distally (tr in Fig. 10B). On the left PM, the median end of such a ridge merges into the proximalmost end of the septum, where the latter becomes confluent with the medio-distal part of the scutular rim. Two slightly curved ridges on internal side of the left PM plate.

poorly developed or absent on the right PM, running almost parallel to each other or strongly diverging medio-laterally, and less robust than proximal part of septum; distal ridge (dr in Fig. 10B) projecting proximo-distally or transversely along gently curved direction from lateral wall of scutular rim to lateral margin of both PM plates where it widens and becomes less pronounced; distal ridge of left PM probably corresponding to accessory septum of Ubaghs (1967) (= posterior boundary of left pharynx of Jefferies, 1986); proximal ridge (pr in Fig. 10B) slightly shorter than distal ridge, almost straight and parallel to proximal margin of each of the two PM plates. Right PM differing from left PM in the small pit (= infundibulum of Ubaghs, 1967 and pit for dorsal end of lateral line ganglion of Jefferies, 1986) lying proximo-lateral to right scutula (Fig. 8C). Shallow groove (sg in Fig. 10B) for articulation with C20 and C22 running parallel to lateral part of proximal margins of left and right PM, and becoming progressively shallower near its lateral end; median end of groove interrupted by small ridge projecting latero-medially from medio-proximal part of scutular rim to lateral angle of external margin of excavation for appendage articulation (= cerebral basin of Jefferies, 1986). Proximalmost part of internal side of lateral margin of left and right PM showing 'step' ('s' in Fig. 10B) delimiting sudden change in the curvature of this margin and presumably representing interlocking articulation with left and right PLM respectively. Median part of both left and right scutular rim merging medially into transversely expanded area occupying median 1/3 of internal margin of excavation for appendage articulation, and presumably representing basal portion of each of the 2 apophyseal horns (Ubaghs, 1967) (=hypocerebral processes of Jefferies, 1986) (ah in Fig. 10B), not preserved in available material. Excavation on both PM plates consisting of shallower distal and deeper proximal parts; distal part (=prosencephalar part of cerebral basin of Jefferies, 1986) delimited by internal margin of excavation and by thin ridge running along slightly oblique direction from bases of apophyseal horns to proximo-medial angle of both plates; distal part (=deuterencephalar part of cerebral basin of Jefferies, 1986) delimited by above mentioned thin ridge and by external margin of excavation.

*Convex surface.* Cup-like co-operculum (Ubaghs, 1967) (= dorsal calcitic cup of pyriform body of Jefferies, 1986) near proximo-lateral angles of C20 and C22 (Figs 8B-D, 9A), delimited by rim with thicker proximo-lateral and thinner medio-distal margins; rim interrupted medially by short, deep, transverse sulcus extending from excavation of co-operculum to portion of inner surface between co-operculum and proximal margins of C20 and C22; at the level of sulcus, both ends of co-opercular rim continue medially into slightly raised ridges parallel to median excavation of proximal margin of C20 and C22, gently convex distally and delimiting very shallow groove. Lateral wall of left and right co-opercula merging gradually into proximalmost part of lateral margin of both C20 and C22. Lateral 1/2 of proximal 1/3 of internal surface of both plates much deeper than the rest of the internal surface and showing 2 ridges (=? n1 and n3 branches of palmar complex of Jefferies, 1986) projecting from distal wall of co-operculum, running close to each other distally for a short distance, then bending slightly medially and diverging from each other before disappearing abruptly medially (Figs 8C-D, 9A). Proximo-lateral part of co-opercular rim of C20 (Figs 8B, D, 9A) housing small subcircular pit (= pit of lateral line ganglion of Jefferies, 1986), c. 1/3 size of co-operculum and corresponding in position to infundibulum on inner surface of right PM. Straight, poorly pronounced ridge (= ? ventral anterior boundary of posterior coelom of Jefferies, 1986) running obliquely from a point just distal to each co-operculum to median margin of C20 and C22, at c.45° to longitudinal body axis (Fig. 8D). Transversely elongate facet for articulation with PM plate visible along lateral 1/2 of distal margins of C20 and C22, immediately proximo-lateral to co-opercula.

*Stereom.* Internal texture of subcentral and lateral marginal elements of plano-concave surface resembling external texture in the radial arrangement of trabeculae and pores (Figs 7A-B, 8A). Stereom of inside of left and right PM (Figs 8C, 10A) consisting of irregular meshwork of stout trabeculae and extremely irregular pores of different shapes and sizes, replaced by more compact texture on septum, scutular rim and bases of apophyseal horns as well as along proximal edge of both PM plates. Elongate, sometimes confluent pores along proximal and distal ridge on lateral half of PM plates. Stereom of excavation for appendage insertion with generally small, rounded pores and thin trabeculae (Figs 8B, D, 9A, 10A). Texture of inside of C20 and C22 consisting of regularly arranged circular pores, slightly smaller peripherally than

centrally. Stereom of co-opercula compact (Figs 8B-D, 9A).

APPENDAGE. *Proximal part.* 5-6 tetramerous rings overlapping each other proximo-distally; degree of overlap greater proximally than distally; distalmost ring slightly smaller than others and tightly wrapped around proximal styloid process; latero-distal angles of ring plates gently rounded (Figs 2A-B, 4B, D, F, 5A-D, 6A, C).

*Intermediate part.* Styloid with robust, stout proximal blade, triangular in section, less expanded transversely than distal blade and carrying a blunt apex; distal blade slightly bent towards the proximal blade in lateral view and with small, flat, triangular distal bearing surface. Sharp longitudinal keel running between the two blades, with parabolic outline in lateral view. Lateral styloid surfaces gently concave (Figs 5A-D, 12C).

*Distal part.* Few proximal ossicles preserved (mostly disarticulated), subrectangular in lateral view and apparently poorly developed, blunt apexes, except in the first two ossicles, possibly carrying a small distal bearing surface (Figs 7A,B, 12A-D).

*Stereom.* Minute pores and thin trabeculae centrally on proximal ring plates and styloid; more compact stereom near margins of ring plates and on ossicles.

REMARKS. *Adoketocarpus acheronticus* displays little morphological or ontogenetic variation, as evidenced by small changes in the shape and proportions of several isolated skeletal elements of different sizes, which presumably belong to individuals of different ages, and by the similar proportions of complete specimens. The largest known individuals are either pyriform or ovato-lanceolate, whereas small to medium-sized individuals are only slightly longer than wide and their lateral margins are convex. Such differences are only partly caused by deformation. Deformation is, however, negligible in most cases, as the specimens are often found slightly disrupted but without signs of breakage. Likewise, disarticulated plates lying in proximity to each other are rarely broken; often, they are turned upside down or slightly rotated.

The right LOP, A, left and right PLM, left and right PM and C20 and C22 plates are most variable. The right LOP is sutured to the rest of the skeleton in most specimens, slightly displaced in a few specimens and rarely isolated. In the smallest specimen (Fig. 4C,F), the right LOP is more asymmetrical and elongate proximo-distally than in larger specimens (Figs 4A-B, D-E, 7B, 8A); its distal process is distinctly triangular with a blunt, latero-distal angle, and its latero-distal margins are deeply embayed. Together with the left PM, this is the largest element of the plano-concave surface. The distal process and bilateral symmetry of the right LOP vary in larger specimens. Thus, in some individuals the right LOP becomes almost bilaterally symmetrical (Figs 4D-E, 7B, 8A), whereas in others left and right latero-distal margins of this plate differ in length and orientation with respect to the longitudinal body axis, so that its distal process is displaced with respect to this axis (Figs 4A,B, 11A).

The outline of plate A varies from subrectangular in small and medium specimens to elongate pentagonal or subtriangular in large individuals (Fig. 4A-E).

The PLM plates have 3-4 sharp, proximal lateral serrations with steep distal margins in small to medium specimens; in large specimens, the serrations are more numerous, blunt-ended and with less steep distal margins; size of the serrations does not seem to change at different ontogenetic stages (Figs 4A-E, 5C).

In the smallest individual (Fig. 4C,F), distal margins of the PM plates are much shorter than proximal margins, and the proximal excavation for insertion of the articulated appendage is shallower than in larger individuals.

Plates C20 and C22 are 2.5-3 times as long as wide and differ mainly in degree of curvature of their lateral margins and in length and orientation of their medio-distal margin. One isolated C20 (Fig. 8B) has a more elongate and concave medio-distal margin and broad median emargination in its proximal margin. In the same plate, a ridge runs for c. 2/3 plate width from the proximal end of its medio-distal margin to a thickened triangular area latero-distal to co-operculum; median 2/3 of ridge almost straight; lateral 1/3 bent strongly towards co-operculum. Shallow areas present just proximal to the ridge, and delimited proximally by a second, fainter transverse ridge running from median margin of C20 to a point c.1/2 along maximum plate width before disappearing abruptly laterally.

**Adoketocarpus janeae** sp. nov.
(Figs 11B,C, 12E, 13)

ETYMOLOGY. For Jane Jell, who helped collect the material described herein.

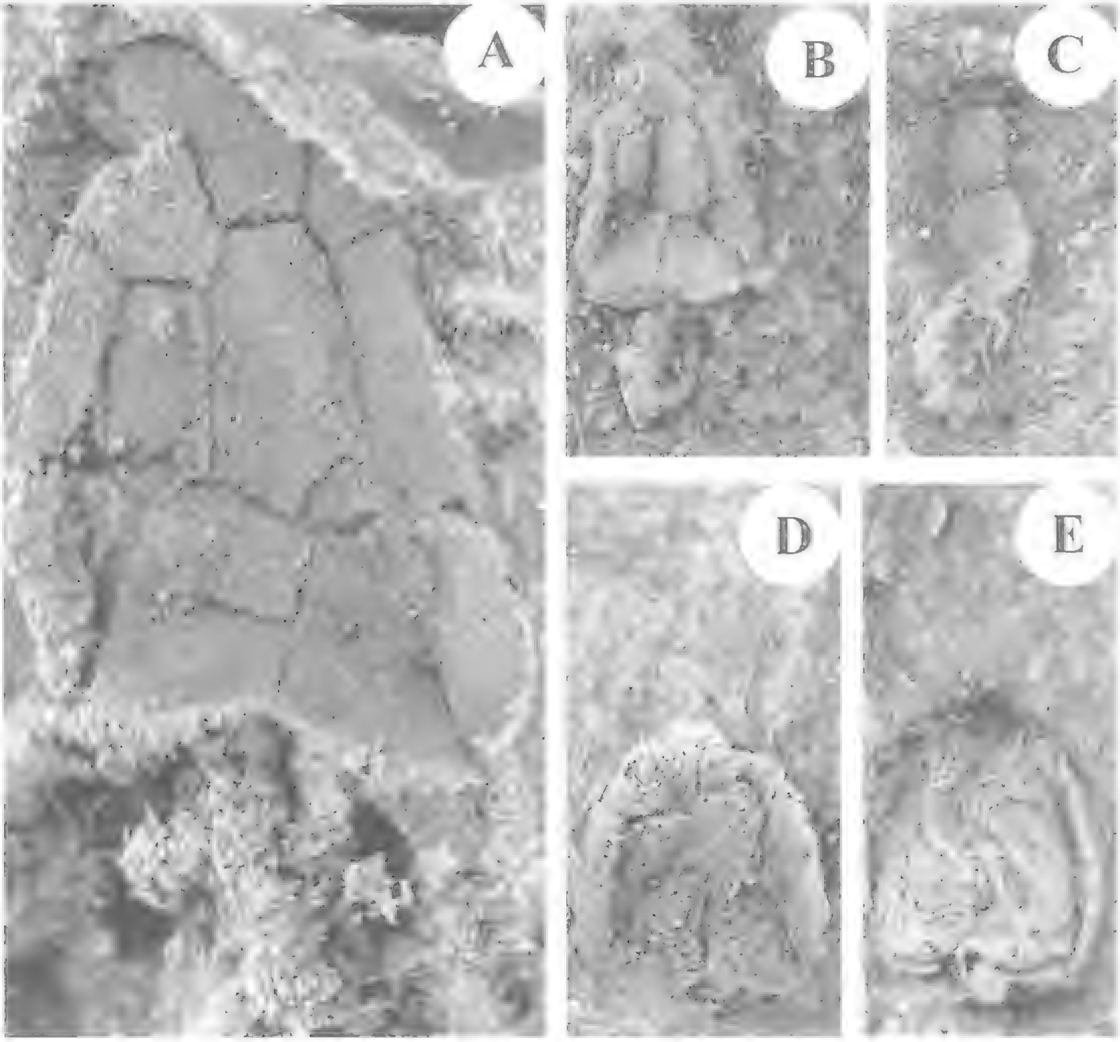


FIG. 11. A,D,E, *Adoketocarpus acheronticus* gen. et sp. nov., from NMVPL1927. A, plano-concave surface of QMF37208, ×9. D,E, plano-concave and convex surfaces of QMF37214, ×12. B,C, *Adoketocarpus janeae* gen. et sp. nov., from NMVPL252, plano- concave and convex surfaces of NMVP149391, ×12.

MATERIAL. Holotype: NMVP100359. Paratype: NMVP100360 from NMVPL1924 on Mathieson's Creek north of Kinglake West (=T95 of Williams 1964); NMVP149391, 149392 from NMVPL252.

DIAGNOSIS. Lateral margins almost straight. Left DLM and right EXM/ILM subequal in length. Left LOP and right DLM smaller than other marginal plates and approximately equal in size. Left LOP median to left latero-distal angle of plano-concave surface. Plate A narrow and elongate. Plate C slightly wider proximally than distally.

DESCRIPTION. General aspect. Only those skeletal features which distinguish *A. janeae* from *A. acheronticus* are discussed in detail here.

Lateral margins of body straight for most of their length and only slightly converging distally. Left DLM and right EXM/ILM much longer than wide and of similar shape and size; distal margin of left DLM at 45° with longitudinal body axis. Free margins of left LOP (distal in position) and of right DLM gently convex; free margin of right DLM about 3 times as long as medio-proximal margin. Left LOP lying median to left latero-distal angle of plano-concave surface and contributing only to a small extent to left lateral

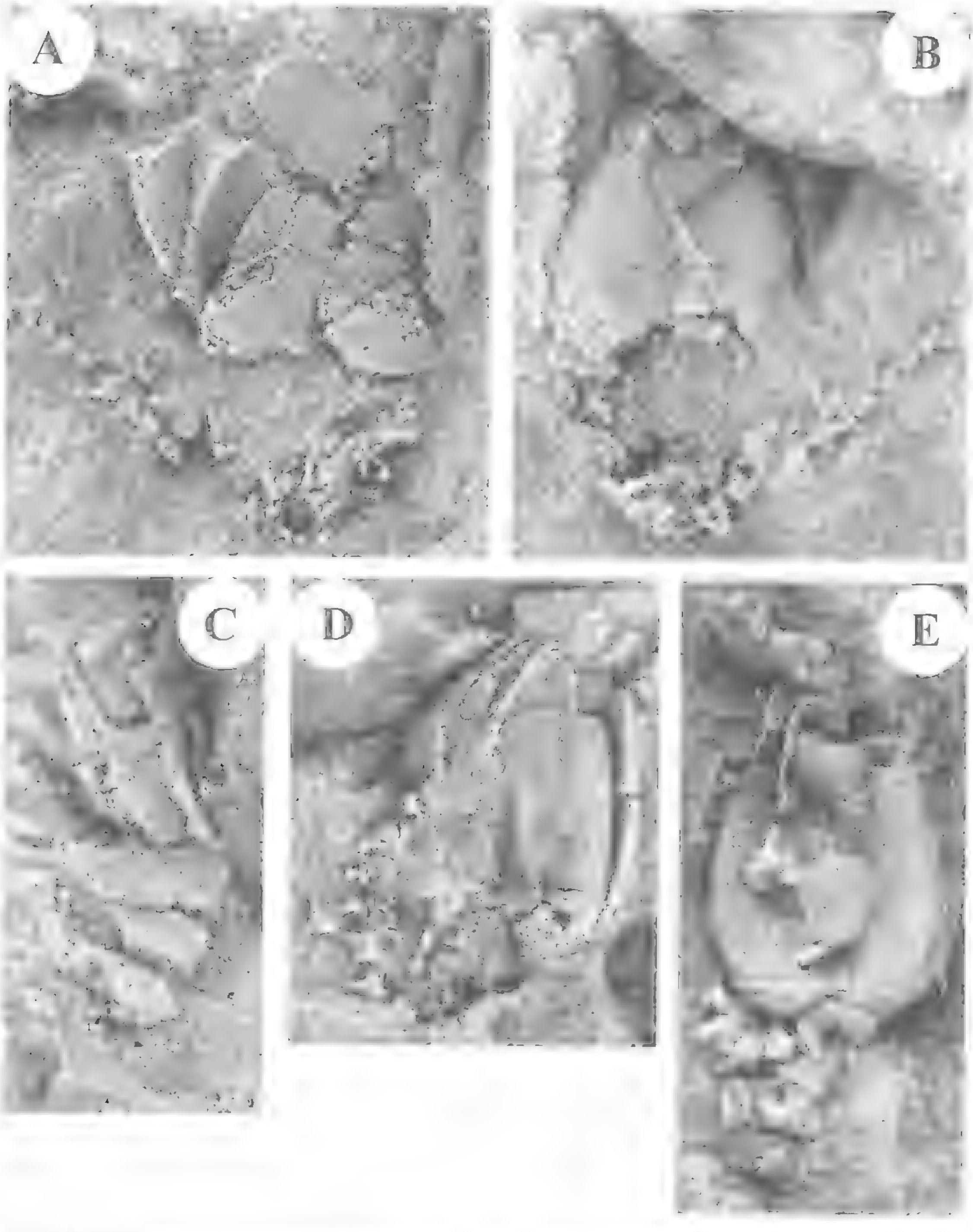


FIG. 12. A-D, *Idoketocarpus acherontieus* gen. et sp. nov., from NMVPL1927, ×10. A-B, disrupted body and appendage QMF37202. C, isolated styloid and ossicles QMF37213. D, partial convex surface and ossicles QMF37212. E, *Idoketocarpus janeae* gen. et sp. nov., disrupted convex surface of NMVP149392 from NMVPL252, ×10.

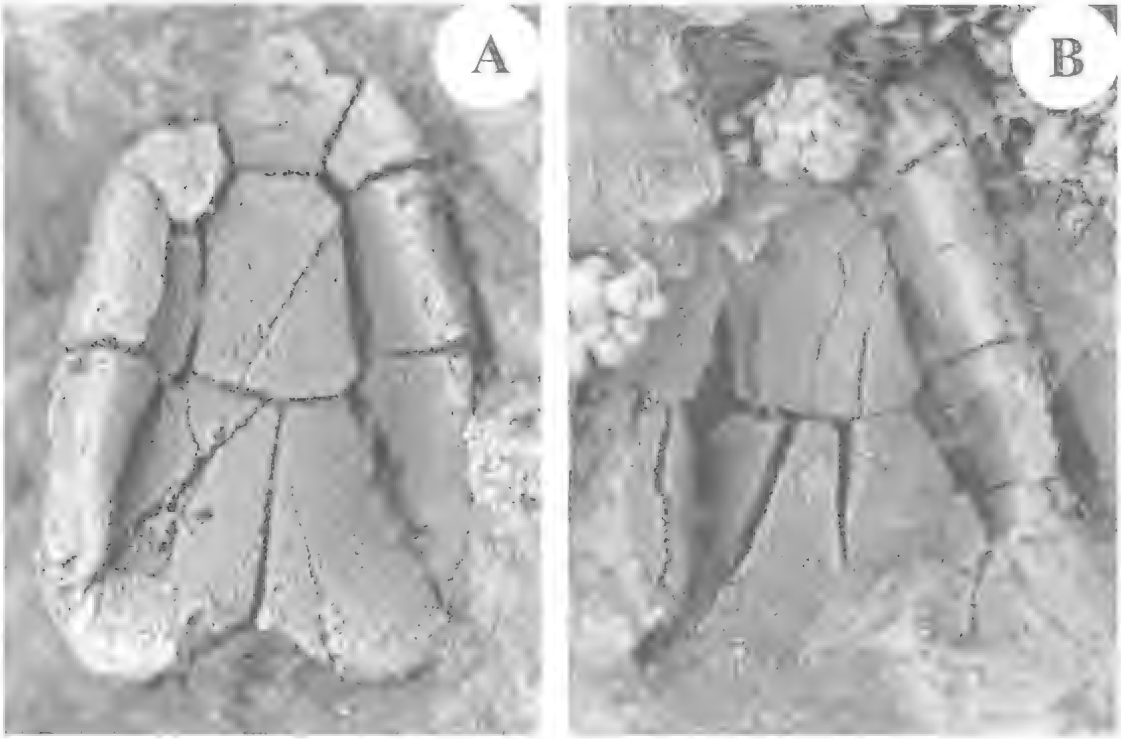


FIG. 13. *Adoketocarpus janeae* gen. et sp. nov., from NMVPL1924. A, NMVP100359, holotype, almost complete, slightly disrupted, plano-concave surface, ×10. B, NMVP100360, partially disrupted, incomplete, plano-concave surface, ×10.

body margin. Right LOP with semi-elliptical distal process and markedly sinuous proximo-lateral margins, and c.1/2 as large as C; left latero-distal margin of right LOP at c.120° with free margin of left LOP. Lateral 1/2 of proximal margin of each of the 2 PM plates passing gradually into median 1/2; the latter only slightly concave and meeting its antimere at c.120°; suture between left and right PM straight. C slightly wider proximally than distally. Suture between A and C gently concave leftward throughout most of its length. Plate A at least 3 times as long as wide and in contact with left arm of distal, chevron-shaped margin of left PM along very short suture. Robust, sharp serrations partly visible along disrupted lateral margin of right PLM in the less complete of the 2 specimens observed. Stereom structure of coarse pores and irregular, sinuous trabeculae; pores decreasing in size towards plate sutures.

*Measurements.* NMVP100359 (Fig. 13A) is 5.7mm wide and 7.8mm long.

REMARKS. Attribution of the Lower Devonian species to *Adoketocarpus* is based on the plating pattern of the plano- concave surface, but only 4 individuals permit limited comparisons with the type species. The differences between the Lower Devonian and the Upper Silurian taxa warrant a distinct specific assignment for the former.

Such features of *A. janeae* as shape and relative proportions of left LOP and left DLM and high length/width ratio of A are similar to those in *E. savilli* Beisswenger, 1994 from the Llandeilo of Morocco (Fig. 3C). In *E. savilli* and *A. acheronticus*, the left LOP builds the left latero-distal angle of the plano-concave surface and the most proximal part of its lateral margin contributes to the left lateral body wall. In both species, the left latero-distal margin of the right LOP and the free margin of the left LOP meet at an obtuse angle. In *A. janeae*, the left LOP lies almost completely median to the left latero-distal angle of the plano-concave surface and its free margin is at c.120° with the left latero-distal margin of the right LOP. *Adoketocarpus janeae* shows a more bilaterally symmetrical body outline than either *A. acheronticus* or *E. savilli* (Figs 3C,D, 13A), although elements of asymmetry are evident in the arrangement of the distal marginal

plates of the plano-concave surface and in the different length of the left and right lateral margins of the body.

The higher degree of bilateral symmetry of *A. janeae* is also observed in the shape of the right LOP, the distal process of which lies only slightly to the left of the longitudinal body axis. Because the only convex surface of *A. janeae* is not well preserved (Fig. 12E) its degree of asymmetry is uncertain.

## COMPARISONS BETWEEN *ADOKETOCARPUS* AND OTHER PARANACYSTIDS

Members of the Paranacystidae Caster, 1954 (Ruta, 1997c) are readily identified by several features such as the plate configuration of the convex surface and the 2 unequal subcentral plates on the plano-concave surface. As defined by Caster (1954) the family includes *Paranacystis petrii* Caster, 1954, *P. simoneae* Ruta, 1997c, *Adoketocarpus acheronticus* and *A. janeae*. Haude (1995) placed *Yachalicystis triangularis* from the Lower Devonian of Argentina in the Paranacystidae, based on the 2 large, proximo-distally elongate plates on the convex surface and on details of the stereom. Ruta (1997c) tentatively assigned the Middle Devonian *Dalejocystis casteri* Prokop, 1963 from Bohemia to the Paranacystidae, based on its overall resemblance to *Y. triangularis*. However, both *Y. triangularis* and *D. casteri* are too poorly preserved for their affinities to be fully evaluated, and will not be considered further here. Because the material of *A. janeae* is incomplete, the following discussion focusses mainly on *A. acheronticus*, except where a direct comparison between the Lower Devonian form and other paranacystids is necessary.

The body outline is more asymmetrical in *A. acheronticus* than in either *Paranacystis* species. With the exception of the left and right PLM, the remaining lateral marginal plates of the plano-concave surface of *A.acheronticus* do not form pairs of elements of similar shape and size, and are smaller than either left or right PLM; conversely, in both *Paranacystis* species, the lateral marginal elements immediately distal to PLM are almost mirror images of each other and comparable in size with these plates. In *A. janeae*, the left DLM and the right EXM/ILM are similar in shape and size.

*A. acheronticus* differs from both *Paranacystis* species in that plate A is only slightly longer than wide and much smaller than C; in addition, C is much wider in *A. acheronticus* than in either *Paranacystis* species; in *P. simoneae*, C has a robust, distal triangular process (Ruta, 1997c).

As in *P. simoneae*, the 2 PLM plates of *A. acheronticus* have a lateral longitudinal row of denticulations. In *P. simoneae*, these are smaller than in *A. acheronticus* and shaped like sub-elliptical, proximo-distally elongate knobs confined to the proximal 2/3 of left and right PLM. In both *Paranacystis* species, the proximal excavation for appendage insertion is wider and deeper than in *A. acheronticus*. The distal, subtrapezoidal plates of the convex surface are much larger with respect to C20 and C22 in *P. petrii* (convex surface not preserved in *P. simoneae*) than in *A. acheronticus*; in addition, the suture formed by the 2 subtrapezoidal plates is shorter in the latter than in *P. petrii*.

For Caster (1954), the distal plates of *P. petrii* were imbricate in life and acted as an ostial cover; he considered this feature diagnostic of the family. *A. acheronticus* suggests that ostial elements identified by Caster (1954: figs 1a-e, 2b) in *P. petrii* are homologous with the left LOP, right DLM and/or right LOP plates. In *A. acheronticus*, the right LOP is tightly sutured with the rest of the plano-concave surface and does not seem to have formed a flexible articulation in life. In a disrupted paratype of *P. petrii* (Caster, 1954, fig. 3b), the distal 1/2 of the internal mould of plano-concave surface shows a subpentagonal plate sutured on the right with a small trapezoidal element. These 2 plates correspond to the right LOP and right DLM of *A. acheronticus* respectively, based on shape and position (see Caster, 1954, fig. 1e). In *A. acheronticus* the distal margins of the left LOP and right DLM are partly visible when the convex surface is oriented towards the observer, suggesting that the so-called ostial elements of *P. petrii* are likely to be displaced and/or disrupted plates of the distal margin of the plano-concave surface.

Distal plate configuration of the plano-concave surface in *A. acheronticus* differs from that of *P. simoneae*, in which C carries a distal triangular process. The shape and position of this process resemble those of the right LOP in *A. acheronticus*; homology of this C process is uncertain. In *P. simoneae*, a small pit near the right proximal angle of the C process occupies the same relative position with respect to the body orifice as the subcircular depression on the underside of the right latero-distal angle of the right LOP of *A.*

*acherontieus*. However, the distal part of the plano-concave surface of *P. simoneae* is not well-known; Ruta (1997c) mentioned the possibility that some skeletal elements (possibly the left LOP and right DLM) in the only known specimen of this mitrate are either displaced or not preserved.

*A. acherontieus* permits a more accurate diagnosis of the Paranacystidae. The distal elements of the plano-concave surface did not act as an ostial cover, as surmized by Caster (1954) in *P. petrii*. Rather, this part of the skeleton was rigid and roofed over the body orifice. The distalmost region of the convex surface, on the other hand, was probably flexible, as indicated by the small, irregular plates surrounding the orifice platelets. This flexible integument is documented in several mitrates (Ubaghs, 1967, 1979; Jefferies & Lewis, 1978; Kolata & Jollie, 1982; Jefferies, 1986; Cripps, 1990; Parsley, 1991; Beisswenger, 1994; Ruta, 1997b).

DISCUSSION. In *A. acherontieus* the simplified plating pattern of the proximal 2/3 of the convex surface is probably a derived condition compared with that of the mitrocystitids and anomalocystitids. On the other hand, the pit on C20 is shared with several mitrocystitids (Chauvel, 1941; Ubaghs, 1961, 1967, 1979, 1994; Cripps, 1990; Ruta, 1997b) which are considered by many workers to be more primitive than the anomalocystitids (Jefferies, 1967, 1968, 1973, 1986, 1991; Craske & Jefferies, 1989; Cripps, 1990; Beisswenger, 1994; Ruta, 1997b, in press; Ruta & Theron, 1997; but see Ubaghs, 1979 and Parsley, 1991).

A twisted orifice at a high angle to the axis of the body is found in *Vizcainocarpus dentiger* (Ruta, 1997b), in young individuals of *Mitrocystites mitra* (Jefferies, 1968; Ubaghs, 1967) and in *Eumitrocystella savilli* (Beisswenger, 1994) among the mitrocystitids, although less pronounced asymmetry of this structure is observed in other mitrates (Thoral, 1935; Ubaghs, 1967, 1969, 1979; Jefferies, 1986).

There are fewer tightly sutured polygonal elements on the plano-concave surface of *A. acherontieus* than on other mitrocystitids or anomalocystitids. The 2 subcentral elements on the plano-concave surface also occur in *E. savilli* and most anomalocystitids, although this condition can be shown to have evolved in parallel in the 2 latter groups (Beisswenger, 1994; Ruta & Theron, 1997; Ruta, in press). In particular, the position of plate A, between C and the left lateral marginal elements of the plano-concave surface, recalls the skeletal configuration of the allanicytidiid anomalocystitids (Ruta & Theron, 1997).

The fewer plates of the convex surface and large C20 and C22 also occur in peltocystid mitrates (Thoral, 1935; Ubaghs, 1967, 1969, Jefferies, 1986; Parsley, 1991); however, these differ from *A. acherontieus* in several aspects of the plating pattern of the plano-concave surface. *A. acherontieus* and *E. savilli* have 2 subcentral, unequal plates on the plano-concave surface and a distal plate roofing over the orifice. In most mitrocystitids and all anomalocysititids, the orifice is delimited by a row of distal marginal plates on the plano-concave surface, consisting of a median (MOP) and two lateral (LOP) elements. Based on topological similarity, Beisswenger (1994) hypothesized that MOP (= plate n) was lost in *E. savilli*, and that the distalmost element of the plano-concave surface is an enlarged and medially displaced right LOP (= plate c of Beisswenger, 1994). This hypothesis was supported by three arguments, two of which also apply to *A. acherontieus*.

His first argument is based on the reconstructed internal features of the distalmost plate of the plano-concave surface of *E. savilli*, which '... carries the beginning of the oblique ridge and builds part of the lateral [body] wall as in other mitrates' (Beisswenger, 1994: 448). Part of the internal side of the plano-concave surface can be observed in *A. acherontieus* (Figs 7A-B, 8A) where the distal end of the oblique ridge is partly visible on the proximal 1/3 of the internal surface of right LOP. The right LOP is larger than the elements lying immediately proximal to it, shows the same spatial relationships with these as in *E. savilli* and closely resembles the like-named plate of the latter in its general shape and in the development of a blunt distal projection covering the orifice platelets. The right LOP of *A. acherontieus* does not contribute to the right lateral body wall to the same extent as its proposed homologue in *E. savilli*, in that it is slightly displaced to the left with respect to the main body axis, presumably as a result of increased torsion of the orifice caused by the loss of a left lateral marginal element.

In *A. acherontieus*, almost the complete course of the oblique ridge is visible on the convex surface as a result of compaction (Figs 4F, 6A, C-D, 7B, 9B), showing that the distalmost end of the ridge lies on the proximal part of the internal surface of the right LOP. On the plano-concave

surface, the suture between the right LOP and C (= plate 12 of Beisswenger, 1994) straddles the distalmost portion of the oblique ridge. The distalmost part of the ridge appears as an impression on the median half of the right distal subtrapezoidal plate of the convex surface.

The second of Beisswenger's (1994) arguments is an hypothesis of morphological transformation inferred from the first argument: loss of MOP and increase in size and leftward displacement of the right LOP would explain leftward twisting of the orifice. If correctly interpreted, this transformation is more evident in *A. acherontieus*, where the orifice opening forms an angle of about 30° with respect to the main body axis, than in *E. savilli*, where this angle is about 45°.

Beisswenger's (1994) third argument is not directly applicable to *A. acherontieus*, as it involves comparison between plate organization on the plano-concave surface of *E. savilli* (Fig. 3C) and *Mitrocystella incipiens* (Fig. 3B) which closely resemble each other in proportions and relative positions of the subcentral and of left and right lateral marginal plates. Comparing these similar arrangements to the more primitive arrangement in *M. barrandei* (Fig. 3A), major differences in the distal 1/3 of the plano-concave surface are interpreted as resulting from loss of plate B (= plate 11 of Beisswenger, 1994) in *E. savilli*. Plate configuration of the distal 1/3 of the plano-concave surface in *A. acherontieus* matches that of *E. savilli*, and suggests that B may be secondarily absent in the Australian taxon.

The number of lateral marginal plates in *A. acherontieus* is reduced by one on the right and on one the left with respect to *E. savilli*, and the relative size and spatial relationships of the elements lying to the left of C are very similar to those of the left LOP, left DLM and A plates (= plates b, 3 and 10 of Beisswenger (1994), respectively). Based on their shape and position, proximal left and right lateral marginal plates correspond to PLM (= plates 1 and f of Beisswenger (1994), respectively). Assuming the correct identification of the other plates, it is reasonable to hypothesize that the left ILM (= plate 2 of Beisswenger, 1994) was lost in *A. acherontieus*, and that such a loss brought A in contact with the left PLM and left PM.

The right lateral marginal plates are more difficult to interpret. Comparison with *E. savilli* indicates that a plate of the right side of the body was lost in *A. acherontieus*. This plate might correspond to the right EXM or ILM (= plates 6 and 7 of Beisswenger (1994), respectively) in *E. savilli* (Ruta, in press), but it cannot be identified unambiguously; hence, our right EXM/ILM notation for the marginal plate lying to the right of C. Finally, the left and right PM correspond to plates i and h of Beisswenger (1994), respectively, based on their shape, position and internal surface.

The resemblance between *E. savilli* and *Adoketocarpus* has implications for the origin and diversification of the Paranacystidae. We propose that the Paranacystidae derive from an ancestor resembling *E. savilli* through a simplification of the plate configuration. Further steps in this lineage may have been the acquisition of bilateral symmetry and a greater elongation of the body. Compensation for the asymmetrical body outline may have been achieved through modification of the relative proportions of the marginal plates of the plano-concave surface. In *A. acherontieus*, plate asymmetries are evident on this surface, but in *A. janeae* and in other paranacystids (Caster, 1954; Ruta, 1997c), such asymmetries disappear or are drastically reduced. Bilateral symmetry probably occurred proximo-distally, affecting the marginal elements first (as in *A. janeae*) followed by the subcentral plates (as in *Paranacystis*).

## CONCLUSIONS

*Adoketocarpus*: 1) is the first representative of the Paranacystidae Caster, 1954 recorded from Australia; 2) from the Upper Silurian predates the next earliest family record in the Lower Devonian of South America (Caster, 1954; Caster & Eaton, 1956; Haude, 1995); 3) provides great detail of its external and internal anatomy, throwing light on several poorly known aspects of the paranacystids and prompting re-interpretation of skeletal organization of the family (Caster, 1954, Haude, 1995; Ruta, 1997c); 4) provides additional evidence of the affinities between Siluro-Devonian mitrates from Australia and those from the Malvinokaffric Realm (Caster, 1954, 1956, 1983; Gill & Caster, 1960; Caster & Gill, 1967; Philip, 1981; Parsley, 1991; Haude, 1995; Ruta & Theron, 1997; Ruta, 1997c); 5) shows that the paranacystids probably evolved from the paraphyletic mitrocystitids; *E. savilli* closely resembles *Adoketocarpus*, especially in the plano-concave surface and in the strongly twisted orifice. Evolution of the paranacystids was characterized by progressive increase in the bilateral symmetry of the body and of the lateral marginal plates.

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## LITERATURE CITED


BEISSWENGER, M. 1994. A calcichordate interpretation of the new mitrate *Eumitrocystella savilli* from the Ordovician of Morocco. Paläontologische Zeitschrift 68: 443-462.

CASTER, K.E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology 34: 1-47.

1954. A new carpoid echinoderm from the Paraná Devonian. Anais da Academia Brasileira de Ciências 26: 123-147.

1956. A Devonian placocystoid echinoderm from Paraná, Brazil. Paleontologia do Paraná (Centennial Volume): 137-148.

1983. A new Silurian carpoid echinoderm from Tasmania and a revision of the Allanicytidiidae. Alcheringa 7: 321-335.

CASTER, K.E. & EATON, T.H. Jr 1956. Microstructure of the plates in the carpoid echinoderm *Paranacystis*. Journal of Paleontology 30: 611-614.

CASTER, K.E. & GILL, E.D. 1967. Family Allanicytidiidae, new family. Pp. 561-564. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1. (Geological Society of America & University of Kansas: New York).

CHAUVEL, J. 1941. Recherches sur les cystoïdes et les carpoïdes armoricains. Mémoires de la Société Géologique et Minéralogique de Bretagne 5: 1-286.

CRASKE, A.J. & JEFFERIES, R.P.S. 1989. A new mitrate from the Upper Ordovician of Norway, and a new approach to subdividing a plesion. Palaeontology 32: 69-99.

CRIPPS, A.P. 1990. A new stem craniate from the Ordovician of Morocco and the search for the sister group of the craniata. Zoological Journal of the Linnean Society 100: 27-71.

GARRATT, M.J. 1983. Silurian and Devonian stratigraphy of the Melbourne Trough, Victoria. Proceedings of the Royal Society of Victoria 95:77-98.

GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology 41: 5-71.

HAUDE, R. 1995. Echinodermen aus dem Unter-Devon der argentinischen Präkordillere. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 197: 37-86.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3: 1-128.

JEFFERIES, R.P.S. 1967. Some fossil chordates with echinoderm affinities. Pp. 163-208. In Millot, N. (ed.) Echinoderm Biology. (Academic Press: London).

1968. The Subphylum Calcichordata (Jefferies 1967) – primitive fossil chordates with echinoderm affinities. Bulletin of the British Museum (Natural History), Geology Series 16: 243-339.

1973. The Ordovician fossil *Lagynocystis pyramidalis* (Barrande) and the ancestry of *Amphioxus*. Philosophical Transactions of the Royal Society of London, Series B 265: 409-469.

1986. The ancestry of the vertebrates. (British Museum (Natural History): London).

1991. Two types of bilateral symmetry in the Metazoa: chordate and bilaterian. Pp. 94-127. In Bock, G. R. & Marsh, J. (eds) Biological asymmetry and handedness. (John Wiley & Sons: Chichester).

JEFFERIES, R.P.S. & LEWIS, D.N. 1978. The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. Philosophical Transactions of the Royal Society of London, Series B 282: 205-323.

KOLATA, D.R., FREST, T.J. & MAPES, R.H. 1991. The youngest carpoid: occurrence, affinities and life mode of a Pennsylvanian (Morrowan) mitrate from Oklahoma. Journal of Paleontology 65: 844-855.

KOLATA, D.R. & JOLLIE, M. 1982. Anomalocystitid mitrates (Stylophora, Echinodermata) from the Champlainian (Middle Ordovician) Guttenberg Formation of the Upper Mississippi Valley Region. Journal of Paleontology 56: 531-565.

PARSLEY, R.L. 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). Bulletins of American Paleontology 100: 5-57.

PHILIP, G.M. 1981. *Notocarpos garratti* gen. et sp. nov., a new Silurian mitrate carpoid from Victoria. Alcheringa 5: 29-38.

RUTA, M. 1997a. Redescription of the Australian mitrate *Victoriacystis* with comments on its functional morphology. Alcheringa 21: 81-101.

1997b. A new mitrate from the lower Ordovician of southern France. Palaeontology 40: 363-383.

1997c. First record of a paranacystid mitrate from the Bokkeveld Group of South Africa. Palaeontologia Africana 34: 15-25.

In press. A cladistic analysis of the anomalocystitid mitrates. The Zoological Journal of the Linnean Society.

RUTA, M. & JELL, P.A. 1999. Two new anomalocystitid mitrates from the Lower Devonian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 399-422.

RUTA, M. & THERON, J.N. 1997. Two Devonian mitrates from South Africa. Palaeontology 40: 201-243.

TALENT, J.A. 1967. Silurian sedimentary petrology and palaeontology. Bulletin of the Geological Survey of Victoria 59: 24-29.

THORAL, M. 1935. Contribution à l'étude paléontologique de l'Ordovicien inférieur de la Montagne Noire et révision sommaire de la faune cambrienne de la Montagne Noire. (Imprimerie de la Charité: Montpellier). 363p.

UBAGHS, G. 1961. Un échinoderme nouveau de la classe des Carpoïdes dans l'Ordovicien inférieur du département de l'Herault (France). Compte Rendu Hebdomadaire des Séances de l'Academie des Sciences, Paris 253: 2565-2567.

1967. Stylophora. Pp. 496-565. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York).

1969. Les échinodermes carpoïdes de l'Ordovicien inférieur de la Montagne Noire (France). Cahiers de Paléontologie. (éditions du Centre National de la Recherche Scientifique: Paris). 112p.

1979. Trois Mitrata (Echinodermata, Stylophora) nouveaux de l'Ordovicien de Tchécoslovaquie. Paläontologische Zeitschrift 53: 98-119.

1994. Échinodermes nouveaux (Stylophora, Eocrinoidea) de l'Ordovicien inférieur de la Montagne Noire (France). Annales de Paléontologie. Invertébrés 80: 107-141.

VANDENBERG, A.H.M. 1988. Silurian-Middle Devonian. Pp. 103-146. In Douglas, J.G. & Ferguson, J.A. (eds) Geology of Victoria. (Victorian Division of the Geological Society of Australia: Melbourne).

1992. Kilmore 1:50,000 map and geological report. Geological Survey of Victoria Report 91: 1-86, + map.

WILLIAMS, G.E. 1964. The geology of the Kinglake District, central Victoria. Proceedings of the Royal Society of Victoria 77: 273-328.

WITHERS, R.B. 1933. A new genus of fossil king crabs. Proceedings of the Royal Society of Victoria 45: 18-22.

# TWO NEW ANOMALOCYSTITID MITRATES FROM THE LOWER DEVONIAN HUMEVALE FORMATION OF CENTRAL VICTORIA

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The anomalocystitid mitrates *Victoriacystis holmesorum* sp. nov. and *Pseudovictoriacystis problematica* gen. et sp. nov. are described from the Lower Devonian Humevale Formation of central Victoria. *V. holmesorum* varies consistently from the type species, *V. wilkinsi*, in the size (larger), shape and proportions of some body plates, the larger more robust spines and the shape of ossicles of distal part of appendage. Some specimens have a sinuous to crook-shaped right spine; others have a proximally geniculate right spine; the left spine is more robust than the right and cigar-shaped. *Pseudovictoriacystis problematica* has an unusual plate configuration on convex surface, which consists of 14 plates, without intervening row II, apparently without C16 and C18, and with a greatly elongate C17. Otherwise it is very similar to *V. holmesorum*, especially in distribution of terrace- like ridges and shape and proportions of plates on plano-concave surface. ❒ *Anomalocystitida, Victoriacystis, Pseudovictoriacystis, Devonian, Australia.*

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*Victoriacystis* was the first anomalocystitid described from Australia (Gill & Caster, 1960). The type species, *V. wilkinsi* Gill & Caster, 1960, redescribed by Ruta (1997), occurs in the lower Ludlovian of the Dargile Formation near Heathcote and the Melbourne Formation at Hawthorn, Melbourne. Although the material from the Melbourne suburb of Hawthorn has been considered Lower Silurian (Gill & Caster, 1960; Talent, 1967; Ruta, 1997), it occurs in the Melbourne Formation of Vandenberg (1988) and is thus Ludlovian. Its age is, therefore, similar to that of the specimens from Heathcote. An incomplete and poorly preserved mitrate (NMVP16880, 16881) from the Lower Devonian part of the Humevale Formation near Kinglake West was attributed by Gill & Caster (1960) to *V.* aff. *wilkinsi*. Ruta (1997) considered it inseparable from the type species. However, additional, more complete specimens from the same locality show that the Lower Devonian *Victoriacystis* is specifically distinct.

Herein, we revise the diagnosis of *Victoriacystis* (Gill & Caster, 1960; Ruta, in press), taking account of the Lower Devonian species and newly available specimens of Upper Silurian *V. wilkinsi* which are treated elsewhere (Ruta & Jell, 1999b).

A second Lower Devonian anomalocystitid mitrate genus from the Humevale Formation, known from a single, partially disrupted individual, is similar to the new species of *Victoriacystis* in the plano-concave surface, but has an unusual plating pattern on the convex surface.

## GEOLOGICAL SETTING

Material described, about 30 partially to fully articulated specimens, comes from NMVPL252 (=Davies Quarry (Gill, 1948); =Middendorp's Quarry (Williams, 1964)) on the western branch of Stony Creek, about 1.6km N of Kinglake West State School and 40km NNE of Melbourne; the site is Lochkovian (Gill & Caster, 1960; Strusz, 1972; Vandenberg, 1988; Vandenberg et al., 1976; Holloway & Jell, 1983; Jell, 1983). Fossils are found in a steely grey pyritic siltstone and are concentrated in a few thin bands interspersed through about 30m exposed in the quarry wall. The diverse fossil faunas are considered to be '... pockets of organic debris ... that do not represent natural assemblages' (Jell, 1983: 210) based on disrupted bedding, attitude of various fossilised individuals and the great concentration of animals in a few thin beds.

Analysis of *Gillocystis runcinata* (ophiocistioid), *Hillocystis atracta* (rhombiferan) and *Sphagoblastus adectus* (blastoid) (Jell, 1983) suggests that the animals were probably buried when they were still alive and were flattened or

slightly crushed by pressure from overlying sediment, depending upon the degree of rigidity of their thecae. Plate dislocation is minimal or does not occur at all. Almost complete absence of skeletal disruption, fractured individual plates, preservation of oral and aboral sides as internally contiguous surfaces (e.g. jaw apparatus of *Gillocystis* against inner aboral surface) and collapse of periproctal plates onto internal side of dorsal thecal surface (e.g. *Hillocystis*) indicate that sediment did not usually enter the body cavity and that geostatic compression of skeletons occurred soon after burial and before soft tissue decay.

Mode of preservation of several individuals of *V. holmesorum* is similar to that of *Sphagoblastus* but may differ from that of *Gillocystis* and *Hillocystis*. Most mitrate specimens are preserved as external moulds, often covered with thin layers of iron oxides. As in *Sphagoblastus*, the theca of *Victoriacystis* is a rigid structure composed of tightly sutured polygonal plates. In most cases, both its convex surface and its plano-concave surface are found almost completely articulated. Disruption is minimal and affects mainly LOP, MOP and C1-C9. Such plates generally lie in close proximity to each other and to the rest of the skeleton and their mutual spatial relationships are often almost unchanged.

Fractures occur usually along lateral margins of the plano- concave surface and on plates PLM, C and C20-C22 and are more numerous in the proximal 1/3 of the body, where, as in the case of other mitrates, the skeleton reaches maximum thickness and greatest curvature (Parsley, 1991). Fractures are sometimes visible at junctions between horizontal and subvertical projections of plates DLM, ILM and PLM. In these cases, subvertical projections often lie flush with convex surface plates while retaining their mutual contacts with them. In some specimens, the convex surface is collapsed onto the plano-concave surface and disruption occurs mainly at level of sutures between lateral plates of convex surface and subvertical projections of DLM, ILM and PLM. C17 is often found sutured with C16 and C18 in contrast with the situation observed in other anomalocystitids in which, when present, this plate is rarely in place (Dehm, 1932; Jefferies & Lewis, 1978; Kolata & Jollie, 1982; Parsley, 1991; Ruta, 1997; Ruta & Bartels, 1998). In a number of specimens, one or, exceptionally, both distal spines are found articulated to DLM, or at a short distance from the body. More frequently, both spines are missing.

Few specimens retain intact appendages, and even in those cases, only proximal and intermediate parts are still in place; ossicles and paired plates of distal part are not preserved. Usually, the tetramerous rings of the proximal part are complete but collapsed while retaining their telescopic arrangement. Separation of ring elements is rare as is their preservation as fully undeformed structures. In some specimens, paired plates and ossicles of the distal part are preserved intact and undeformed, albeit rarely articulated with each other. Frequently, plates are disarticulated, collapsed onto the abapical surface of ossicles or missing altogether. Sometimes, paired plates (especially proximal) are found detached from ossicles while still overlapping each other proximo-distally. The ossicles frequently maintain their alignment. Proximal and distal articular surfaces are observed in at least one individual.

Although rare and largely incomplete in their proximal 1/2, internal moulds are sometimes associated with partially disrupted external moulds. Unlike other Lower Devonian echinoderms from the Humevale Formation, *Victoriacystis* has a relatively large, transversely elongate distal orifice through which fine sediment could easily enter the body cavity during burial. Similar preservation is known in other carpoids, both solutes (Jefferies, 1990) and cornute stylophorans (Jefferies, 1968; Woods & Jefferies, 1992).

## SYSTEMATIC PALAEONTOLOGY

External skeletal terminology and plate nomenclature follow Ruta (in press) with modifications as in Ruta & Jell (1999a). Description of internal body anatomy is based on Ubaghs (1968, 1969). Morphological terminology of ossicles is that of Jefferies & Lewis (1978) and Ruta & Theron (1997). The terms 'apical' and 'abapical' indicate the position of structures close to or away from the ossicular process (or apex) respectively. Specimens are deposited in the Palaeontological Collections of the National Museum of Victoria, Melbourne (NMVP) and the locality is registered in the locality register at the same Museum (NMVPL). Study and illustration of skeletal details was made on latex casts whitened with ammonium chloride.

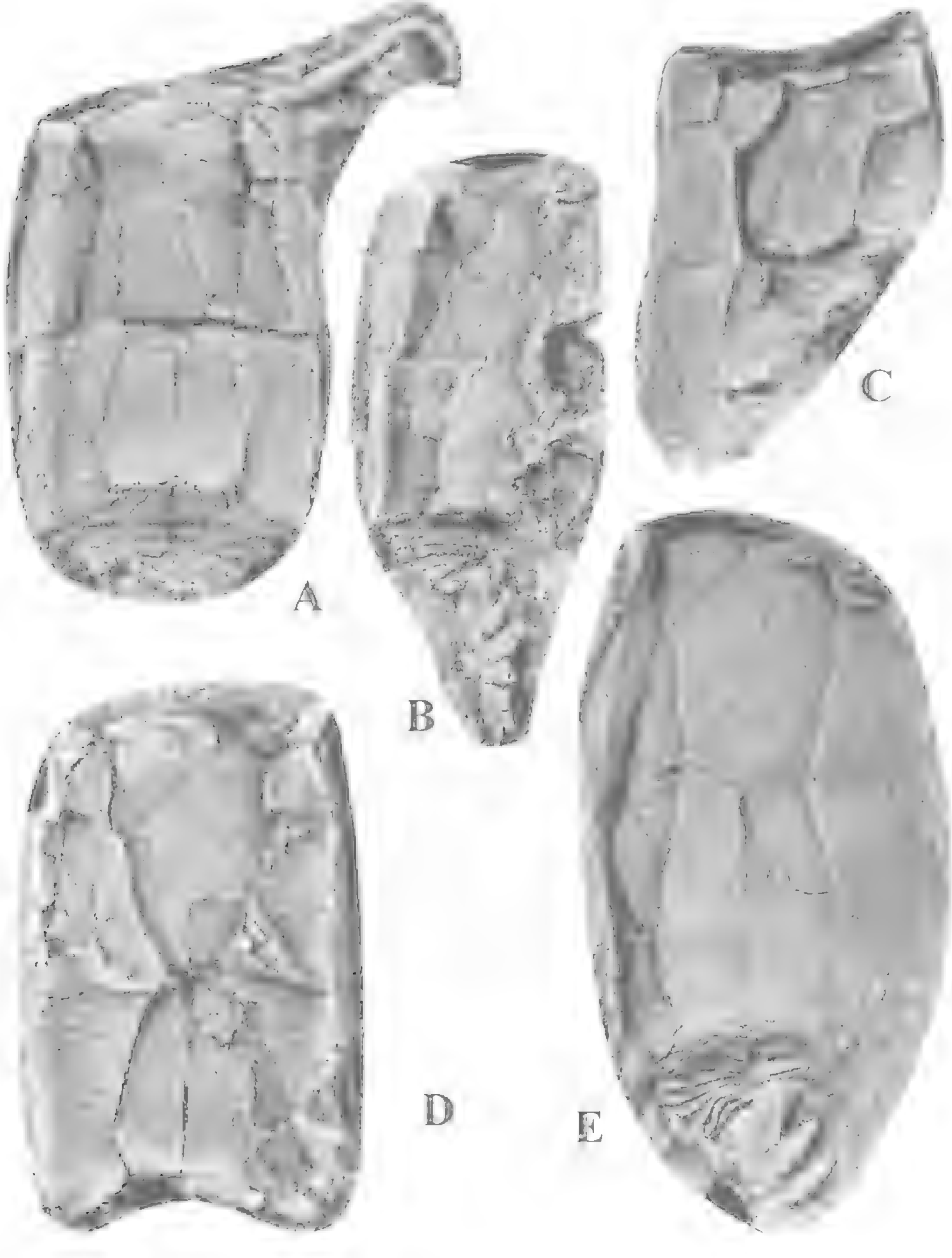


FIG. 1. *Victoriacystis holmesorum* sp. nov. All plano-concave surfaces showing terrace-like ridges, spines, tetramerous rings, styloid and proximal ossicles. A, NMVP100361. B, NMVP100387b. C, NMVP100385. D, NMVP100369. E, NMVP100373. All ×3.

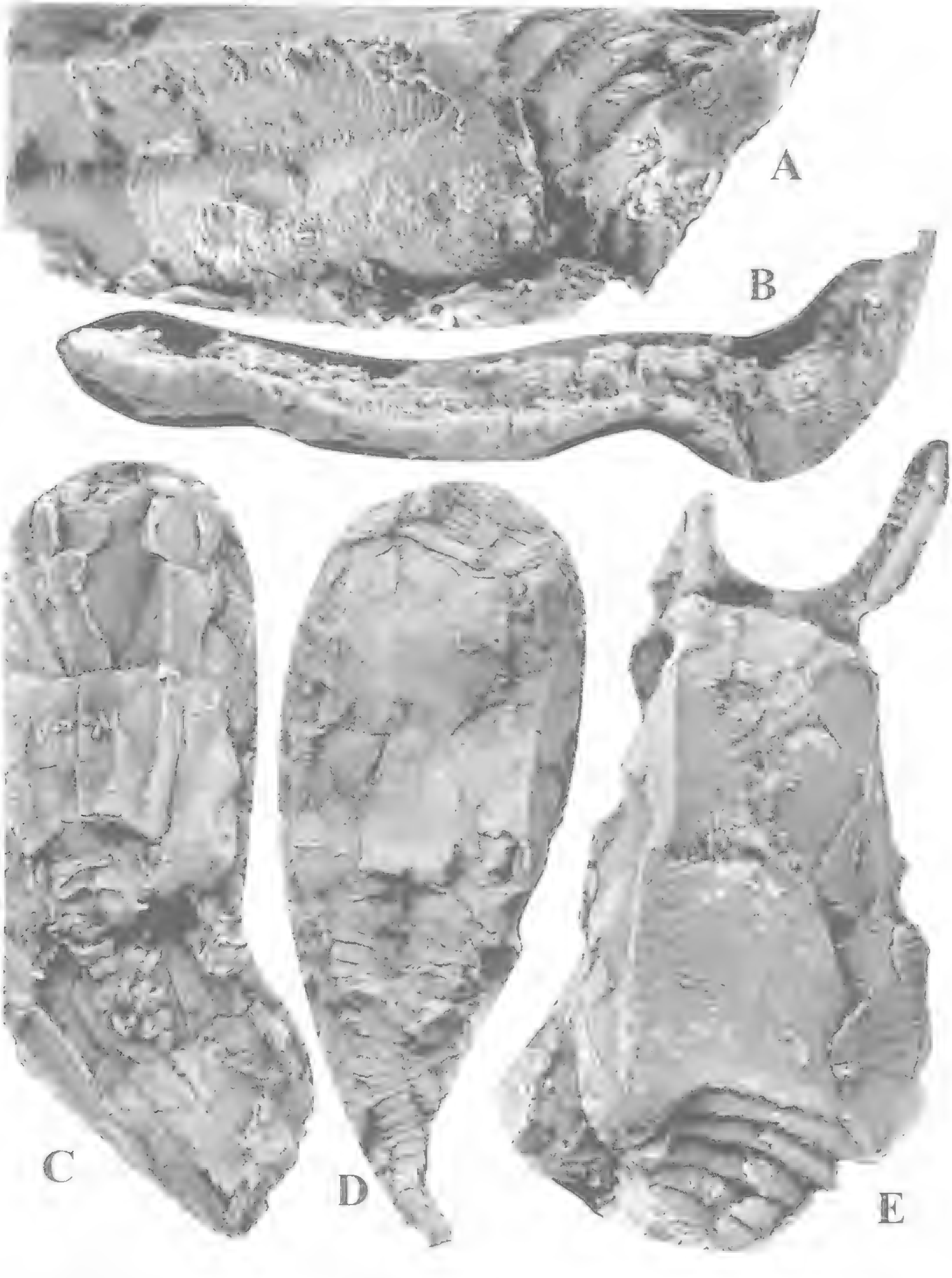


FIG. 2. *Victoriacystis holmesorum* sp. nov. A,E, lateral and plano-concave surface views of NMVP100382, ×5 and ×3, respectively. B, appendage in lateral view of NMVP100371, ×7. C, plano-concave surface of NMVP108627, ×2. D, plano-concave surface of NMVP100378b, ×2

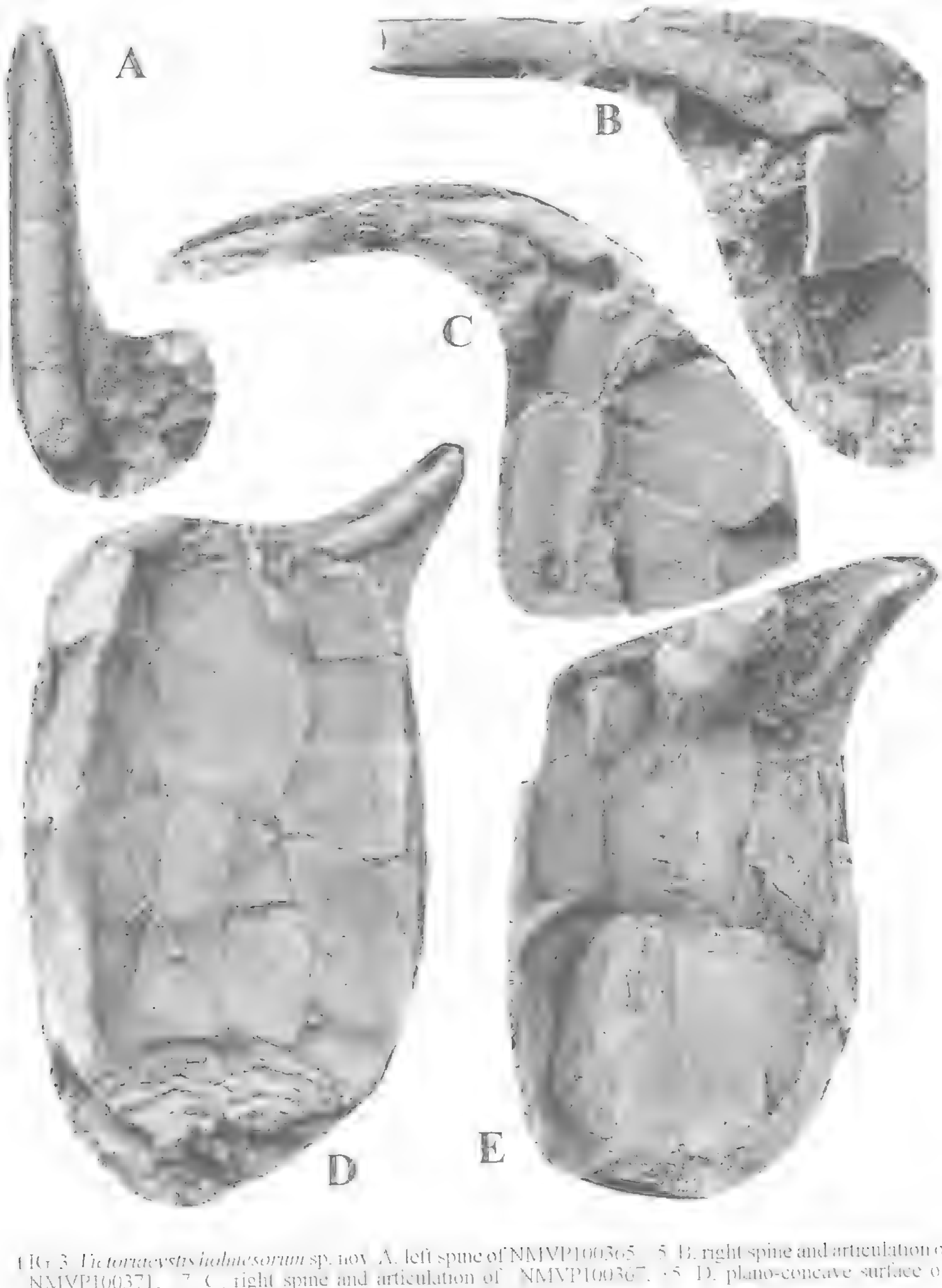


FIG. 3. *Victoriacystis holmesorum* sp. nov. A, left spine of NMVP100365, ×5. B, right spine and articulation of NMVP100371, ×7. C, right spine and articulation of NMVP100367, ×5. D, plano-concave surface of NMVP100381, ×3. E, plano-concave surface of NMVP100384, ×3.

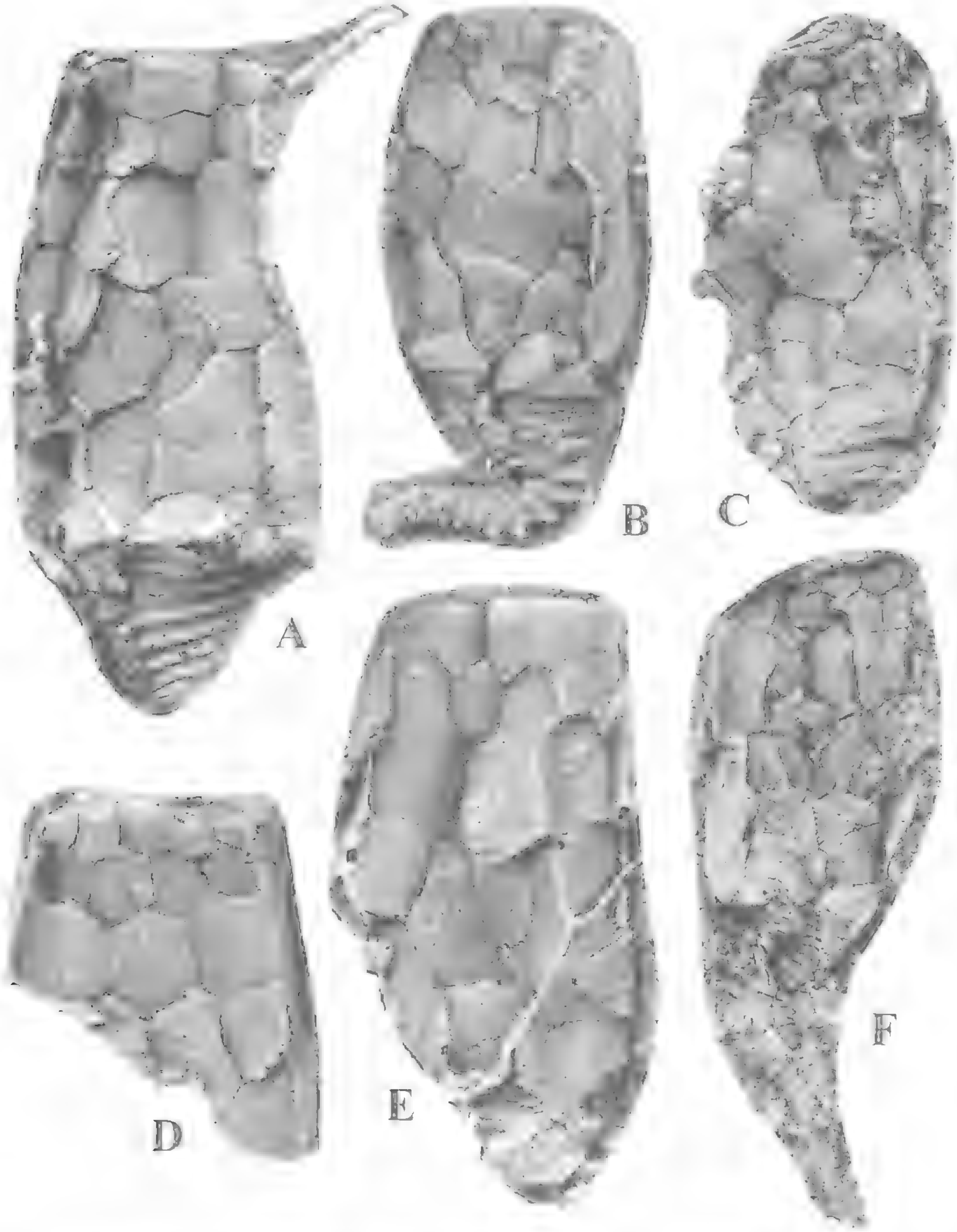


FIG. 4. *Victoriacystis holmesorum* sp. nov. All convex surfaces, showing terrace-like ridges, spines, tetramerous rings, styloid and ossicles. A, NMVP100362, ×3. B, NMVP100363 (holotype), ×2. C, (distally damaged) NMVP100378b, ×2. D, (partial)NMVP100385, ×3. E, NMVP100376, ×3. F, NMVP100374, ×2.

Superorder STYLOPHORA Gill & Caster, 1960
Order MITRATA Jaekel, 1918
Suborder ANOMALOCYSTITIDA Caster, 1952
Family PLACOCYSTITIDAE Caster, 1952

REMARKS. Family groupings in the Anomalocystitida are not satisfactory (Parsley, 1991; Ruta & Theron, 1997; Ruta, in press; Ruta & Bartels, 1998). Analysis of character distribution (Ruta, in press) suggests that, with the exception of the Allanicytidiidae Caster & Gill, 1968, all families, including Placocystitidae as defined by Parsley (1991), are not monophyletic. Parsley (1991) and Ruta (in press) concur in recognising *Victoriacystis* as sister taxon to (*Placocystites* + *Rhenocystis*). However, the allanicytidiids are not closely related to these 3 genera. As Parsley (1991:16) pointed out, their '... assignment to the Placocystitidae is admittedly speculative'. In the light of the revised family concept of Parsley (1991), we restrict this family to *Placocystites*, *Rhenocystis* and *Victoriacystis* only.

**Victoriacystis** Gill & Caster, 1960

TYPE SPECIES. *Victoriacystis wilkinsi* Gill & Caster, 1960 from the early Ludlow Graptolite Beds, Dargile Formation, Victoria; by original designation.

DIAGNOSIS. Rows I-V with 5,4,3,5,3 plates, respectively. C1 and C5 smaller than C2-C4. C17 elliptical to rounded, c.1/2 as long as adjacent C16 and C18. Sutures between C15 and C16 and between C18 and C19 medially convex. C21 shield-shaped to rhomboidal, deeply but not completely inserted between C20 and C22. B absent. A-C suture oblique. Robust, transverse terrace-like ridges mainly confined to C20-C22 and PLM. Lateral margins of PM convex laterally. Tetramerous rings wider proximally than distally, with fold of polyplated integument between rings. Styloid with median longitudinal keel, proximal blade elliptical in section, distal blade spine-like. Successive ossicles decreasing rapidly in size.

**Victoriacystis holmesorum** sp. nov.
(Figs 1-13)

*Victoriacystis* aff. *wilkinsi* Gill & Caster, 1960:54, pl. 10, figs 1, 3.
*Victoriacystis wilkinsi* Gill & Caster. Ruta, 1997:85, fig. 5A.

ETYMOLOGY. For Frank and Enid Holmes, for their assistance in collecting the material.

MATERIAL. HOLOTYPE: NMVP100363. PARATYPES. NMVP100361-100362, 100364-100382, 100384-100389 all from NMVPL252.

DIAGNOSIS. C10, C12 and C14 larger than adjacent proximal and distal plates. Proximal half of C16 and C18 narrower than distal half. C17 not in contact with either proximal angle of C12 or distal angle of C21. A larger than LOP or MOP. Strongly arcuate or geniculate suture between A and C. Distal portion of appendage not differentiated. Styloid large and robust. Proximal ossicular blades strongly recurved. Paired plates distally in appendage without tubercles. Left spine robust, cigar-shaped, >1/2 as long as body, with lateral cutting edge; right spine more slender, sigmoid to geniculate, without cutting edges.

DESCRIPTION. EXTERNAL. *Measurements*. Holotype: body c.28mm long, 15mm wide. Smallest specimen (Figs 1C, 4D): body c.21mm long, 15mm wide. Largest specimen (Fig. 1E): body c.30mm long, 17mm wide.

*Plano-concave surface*. Plano-concave surface subrectangular, slightly wider than convex surface, with sharp lateral margins of 11 marginal and 2 subcentral plates (Figs 1A-E, 2C-E, 3D-E, 12A), with maximum width at or slightly proximal to latero-distal angles of PLM. PM flat, almost as wide proximally as distally, with convex lateral margins except for abrupt curve before joining proximal margin. Curvature of distal margin of left PM usually higher than that of right PM (Figs 1A-E, 2A,C-E, 3D-E, 5D, 6E, 12A). PLM, ILM and DLM with flat horizontal projections; well-developed, subvertical projections with gently convex cross-section and meeting plano-concave surface at 60° (Fig. 12D-E). PLM more than twice as wide distally as proximally, with subvertical projection subtrapezoidal, of uniform depth in distal 1/3, decreasing in depth proximally (Figs 1A-B, 2A, C-E, 3D, 4B, F, 5A-C, 12B). ILM trapezoidal, slightly shorter than PLM, with distally diverging, gently concave medial margins; subvertical projection subrectangular, comparable in size with those of DLM and PLM, with sutural margin in 2 shallow embayments of about same size. DLM irregularly pentagonal, with convex medial margins, with longer less convex lateral margins, with medial 2/3 of distal margin thickened and slightly domed. Subvertical projections subpentagonal, with sutural margin in 2 embayments. Distal surface of DLM vertical or sloping distally towards convex surface, subtriangular, shallower peripherally, with subcentral vertically elongate narrow toroidal process for spine insertion sitting on

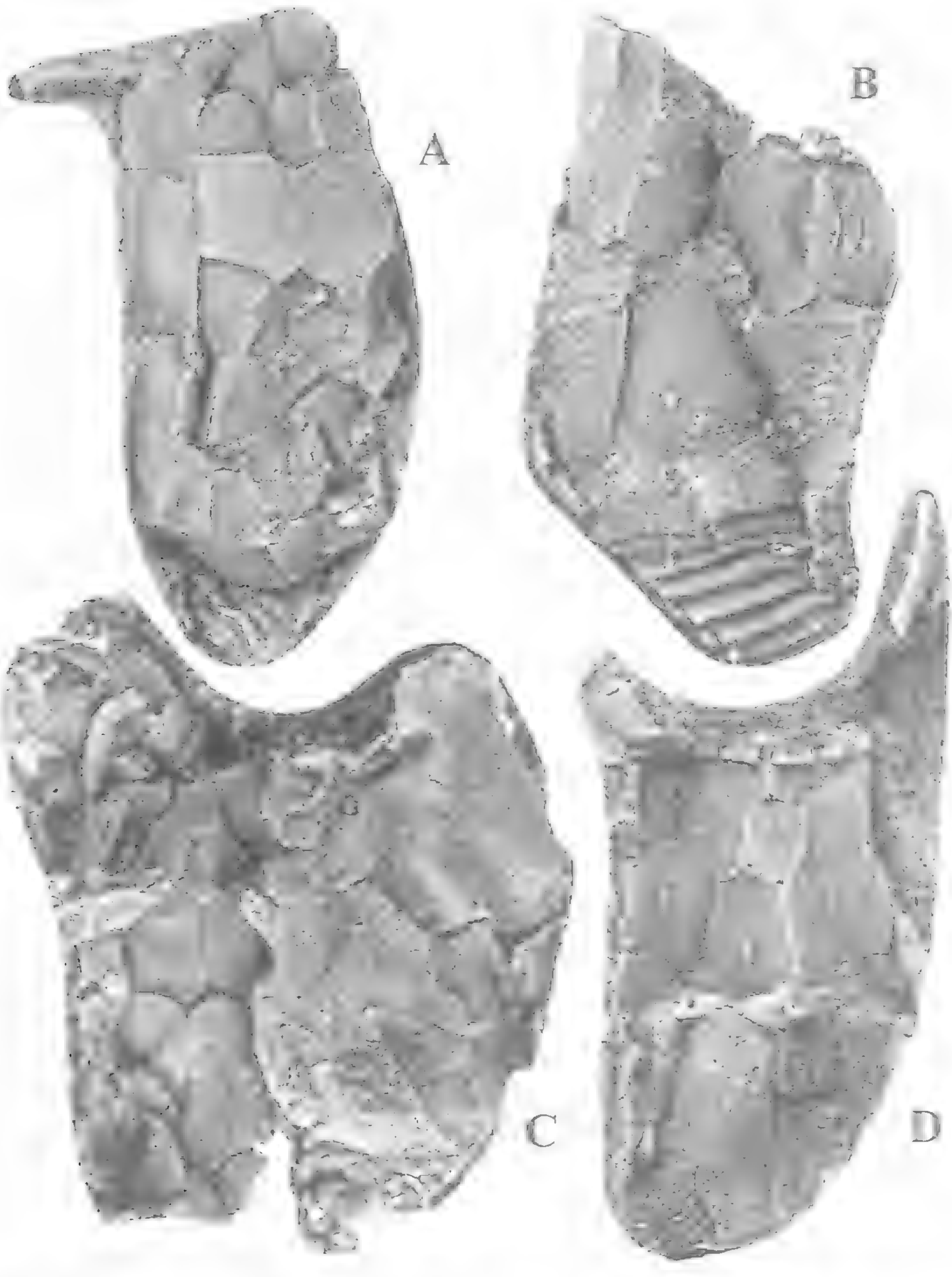


FIG. 5. *Victoriacystis holmesorum* sp. nov. Convex surfaces showing terrace-like ridges, spines, tetramerous rings. A, NMVP100387a. B, (proximal part only) NMVP100382. C, (2 individuals side by side) NMVP108625. D, external of plano-concave surface proximally and inside of convex surface distally of NMVP100376. All ×3.

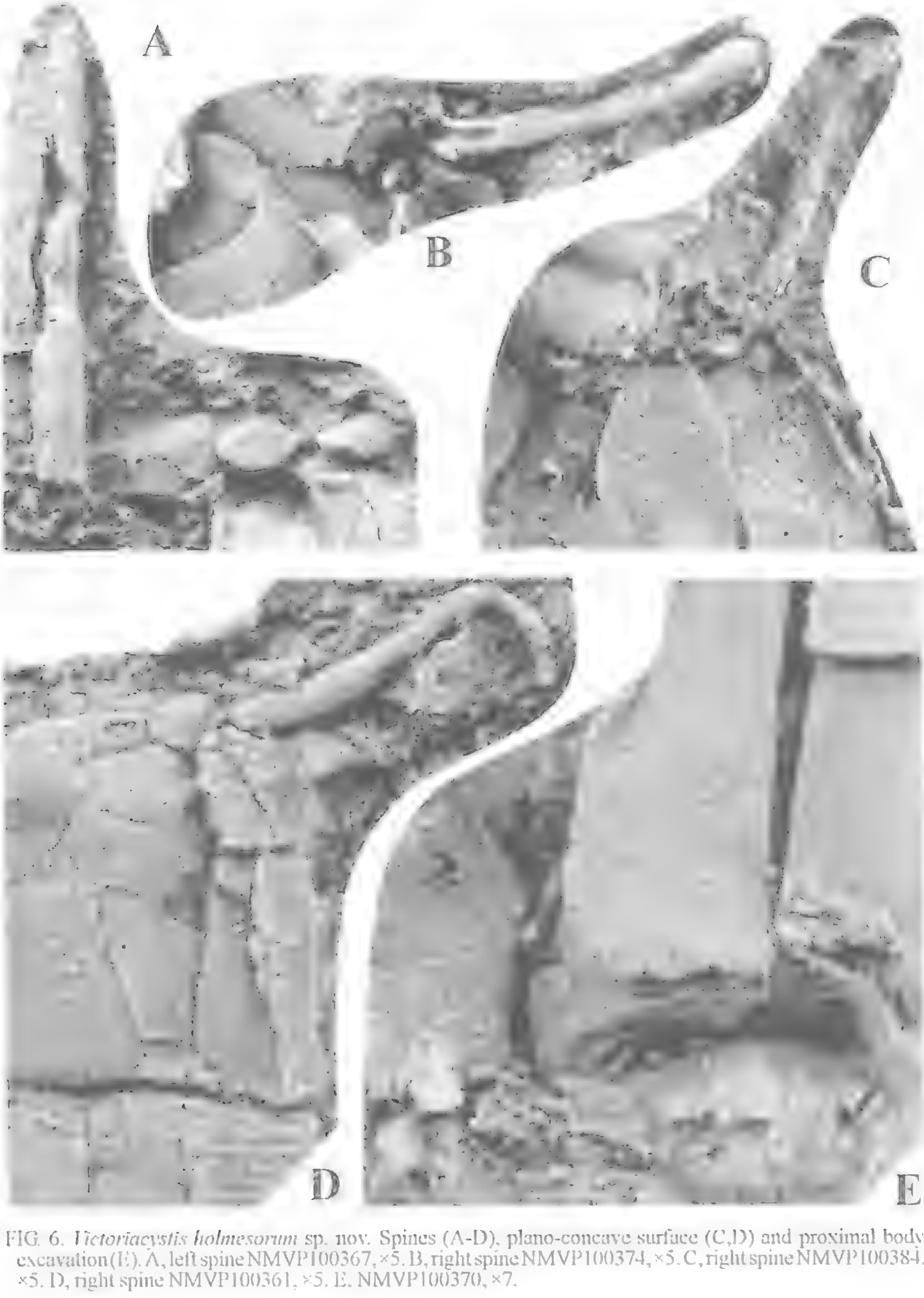


FIG. 6. *Victoriacystis holmesorum* sp. nov. Spines (A-D), plano-concave surface (C,D) and proximal body excavation (E). A, left spine NMVP100367, ×5. B, right spine NMVP100374, ×5. C, right spine NMVP100384, ×5. D, right spine NMVP100361, ×5. E, NMVP100370, ×7.

slightly raised, lens-shaped projection. Small gap between lateral margin of each LOP and medio-distal margin of each DLM (Figs 1A-B, 2A,C, 3D, 4A-B,F, 5A, 11A, 12A). MOP and LOP forming almost transverse row along distal margin. Vertical projections about 1/3 as large as horizontal projections. MOP about twice as wide as each LOP, rectangular, with straight distal margin. LOP c.3/5 size of DLM, subpentagonal, with blunt round latero-distal angles (Figs 1A-D, 2C-D, 6A-B,D, 7A, 12A). Plate A generally subpentagonal to shield-shaped, c.1.5 times as large as each DLM, wedged between left ILM and C, with medial margin arcuate or geniculate, with lateral margin twice as long as latero-distal margin. Plate C largest plate in body, c.1/2 as long and wide as plano-concave surface, with medio-distal margin almost 1.5 times as long as latero-distal margin. Small, round tubercles subcentrally on A and on distal 1/3 of C (Figs 1A,D, 2C, 3D, 6B,D, 7A).

*Convex surface*. 20 plates in 5 transverse rows. Rows II-V gently concave distally. Rows I and IV with 5 plates each. Rows III and V with 3 plates each. Row II with 4 plates (Figs 4A-F, 5A-C, 12C). Maximum convexity c.2/3 of way proximally along C20 and C22 (Fig. 12B). Plates generally decreasing in size distally, except C15 and C19, which are smaller than C10 and C14. C2-C4 subpentagonal, subequal, larger than subrectangular C1 and C5 and just smaller than hexagonal C7 and C8. Distal margins of C1-C5 broadly convex. Lateral margins of C3 usually concave, sometimes straight (Figs 4A-F, 5A,C, 12C). Proximo-medial and proximo-lateral margins of C7 and C8 and proximal margins of C6 and C9 convex. C6 and C9 subpentagonal, often more expanded transversely than proximo-distally (unlike C2-C4), with subparallel laterally diverging (rarely converging) proximal and distal margins (Figs 4A-F, 5A,C, 12C). C10 and C14 wider than long, subhexagonal, with very short medio-distal and medio-proximal margins. C12 hexagonal, slightly wider proximally than distally (Figs 4A-F, 5A-C, 12C). C15 and C19 subtrapezoidal, with convex margins, much wider distally than proximally (Figs 4A-C, D-E, 5A-C, 12C). C16 and C18 with lateral margins strongly diverging proximally, with latero-distal margins 1/2-1/3 length of medio-distal margins. Suture between C16 and C18 extremely short distally, slightly longer in proximal section. C17 subrounded to subelliptical, <1/2 as long as C16 and C18, never in contact with C12 or C21, flat or slightly raised above convex surface (Figs 4A-C,E-F, 5A- C, 8D, 12C). C21 shield-shaped, subhexagonal, with gently convex or rarely straight latero-distal margins meeting at obtuse angle, with proximo-lateral margins straight in distal 1/2 and convex in proximal 1/2 (Figs 4A-F, 5A-C, 8D, 10C, 12C). C20 and C22 largest plates on convex surface, almost twice as long as wide, with oblique distal margins, with convexity of lateral margins increasing slightly proximally (Figs 4A-C,E-F, 5A-C, 7B, 10C, 12C).

*Sculpture*. Terrace-like ridges on PLM (Figs 1A-E, 2A, C-E, 3D-E, 5D, 11C, 12A) and C20-C22 (Figs 4A-F, 5A-C, 8D, 10C, 12A-C), transverse, mostly uniform distance apart, never anastomosing, interrupted abruptly at interplate sutures. Ridges near proximo-lateral angles of PLM, C20 and C22 and near proximal margins of C20 and C22 usually short, interrupted medially, sometimes bifurcating, more crowded together than elsewhere. Bifurcations of ridges rare, in either direction. Ridges on PLM more robust than on C20-C22, with slightly deeper and steeper proximal slope, with distal slope almost flat, slightly convex proximally and gently concave distally. Ridges on C21 variable, with 5-6 most proximal ridges rarely transverse (Fig. 5B), more often convex distally (Figs 4A-C, 8D), with convexity decreasing in straighter more distal ridges, with subcentral ridges straight or chevron-shaped with apex of chevron pointing proximally, with lateral 1/2 of chevron arms transverse or slightly diverging distally, with most distal ridges transverse.

*Body stereom*. Uniformly compact (Fig. 6E) or of minute perforations with irregular outline and no evident distribution pattern (Fig. 8D). Perforations absent or very small along plate margins, frequently replaced by narrow band of short close spaced straight striations. Stereom of centre of plates rarely coarser than peripheral stereom, with more widely spaced larger pores and thicker trabeculae especially on MOP, LOP, A and C (Fig. 1A,D). Stereom of terrace-like ridges on convex surface granular, more compact at free margins. Stereom of ridges on plano-concave surface compact along free margins, coarse and irregularly perforated by small pores on distal 1/2, giving rise to faint striations on proximal 1/2. Striations at c.45° in medio-lateral direction.

*Spines*. Left spine straight, massive, 1/2-5/8 body length, cigar-shaped, tapering to a blunt end in distal 1/3, with cross-section of proximal 2/3 asymmetrical, with semicircular medial margin,

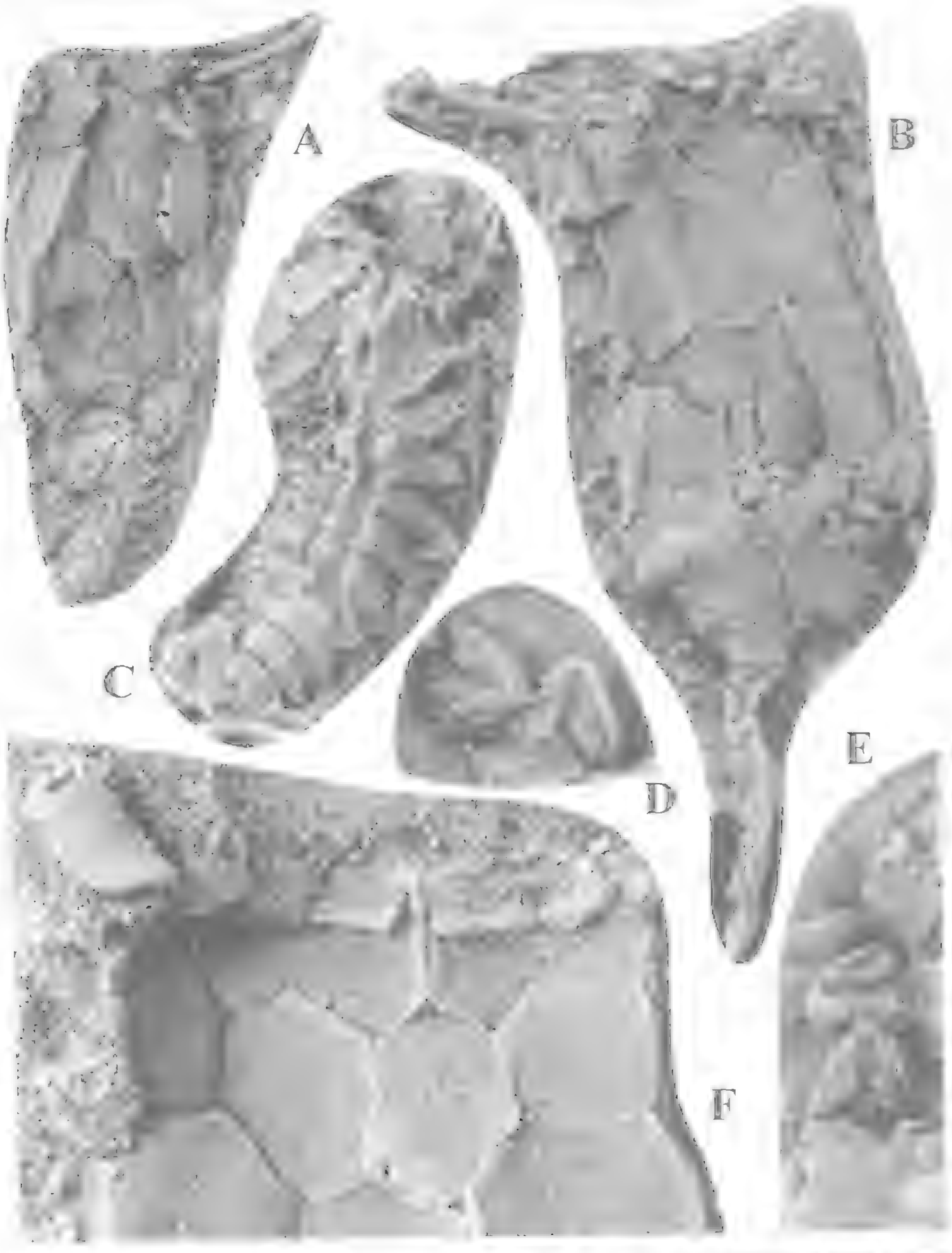


FIG. 7. *Victoriacystis holmesorum* sp. nov. A, plano-concave surface partly disarticulated and with spine. C, detail of proximal appendage of NMVP100374, ×2 and ×5 respectively. B, inside of plano-concave surface of NMVP100371, ×3. D,E, proximal and distal articular surfaces of ossicles, NMVP108627, ×10. F, inside of distal part of convex surface of NMVP100376, ×7.

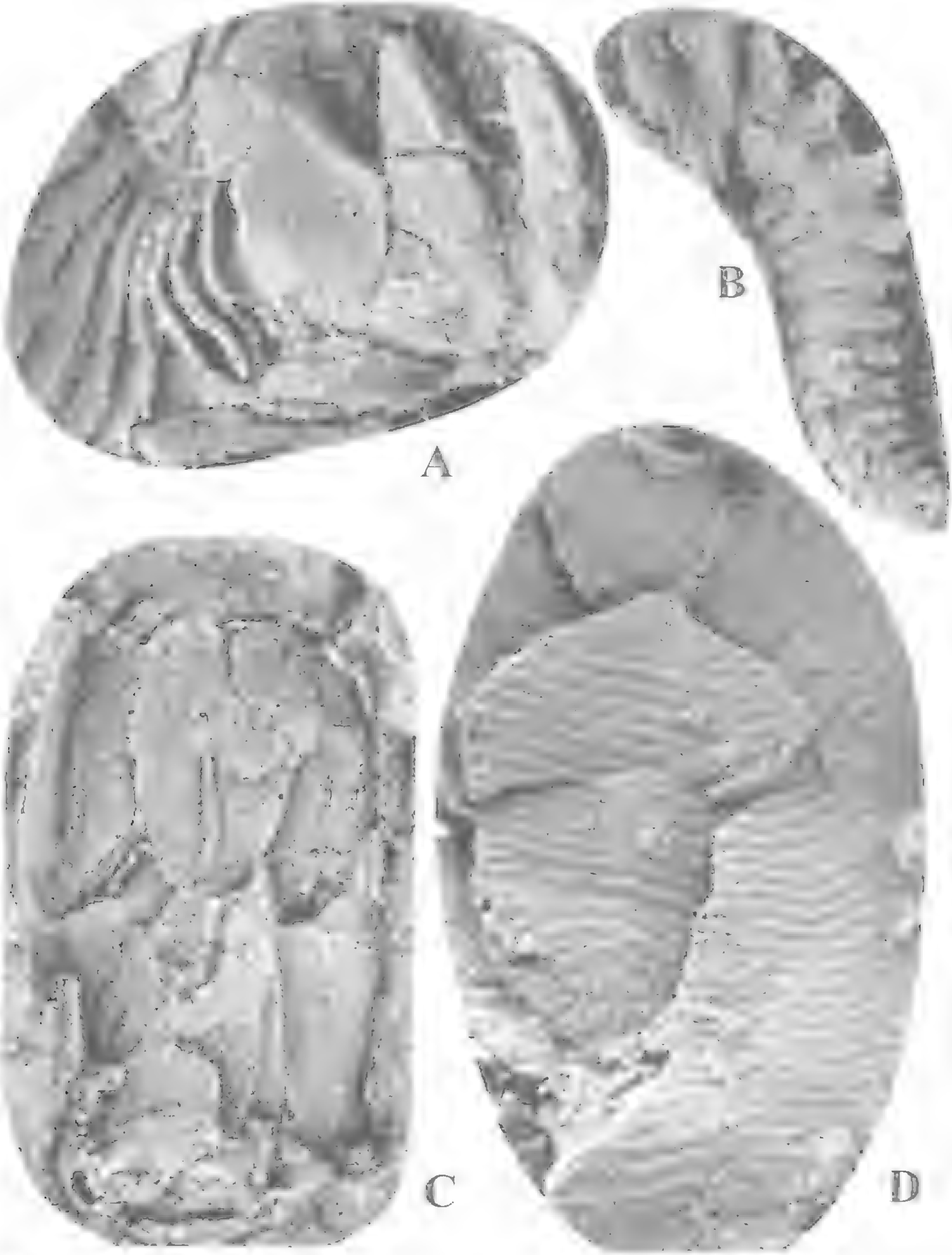


FIG. 8. *Victoriacystis holmesorum* sp. nov. A, tetramerous rings and styloid of NMVP100373, ×10. B, styloid ossicles and paired plates of appendage of NMVP100363 (holotype), ×5. C, inside of plano-concave surface of NMVP100369, ×3. D, proximal surface ornament of NMVP100370, ×7.

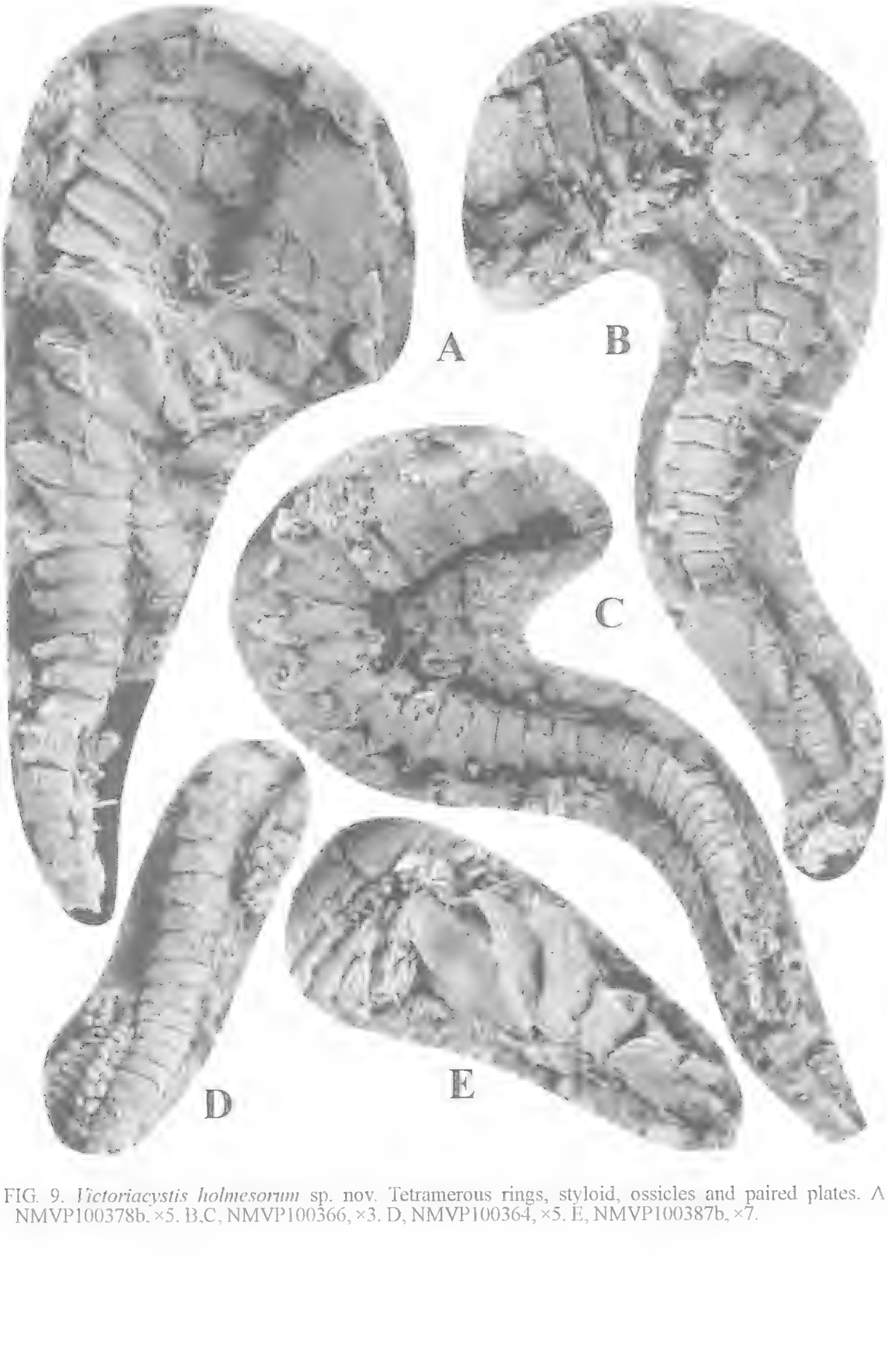


FIG. 9. *Victoriacystis holmesorum* sp. nov. Tetramerous rings, styloid, ossicles and paired plates. A, NMVP100378b, ×5. B,C, NMVP100366, ×3. D, NMVP100364, ×5. E, NMVP100387b, ×7.

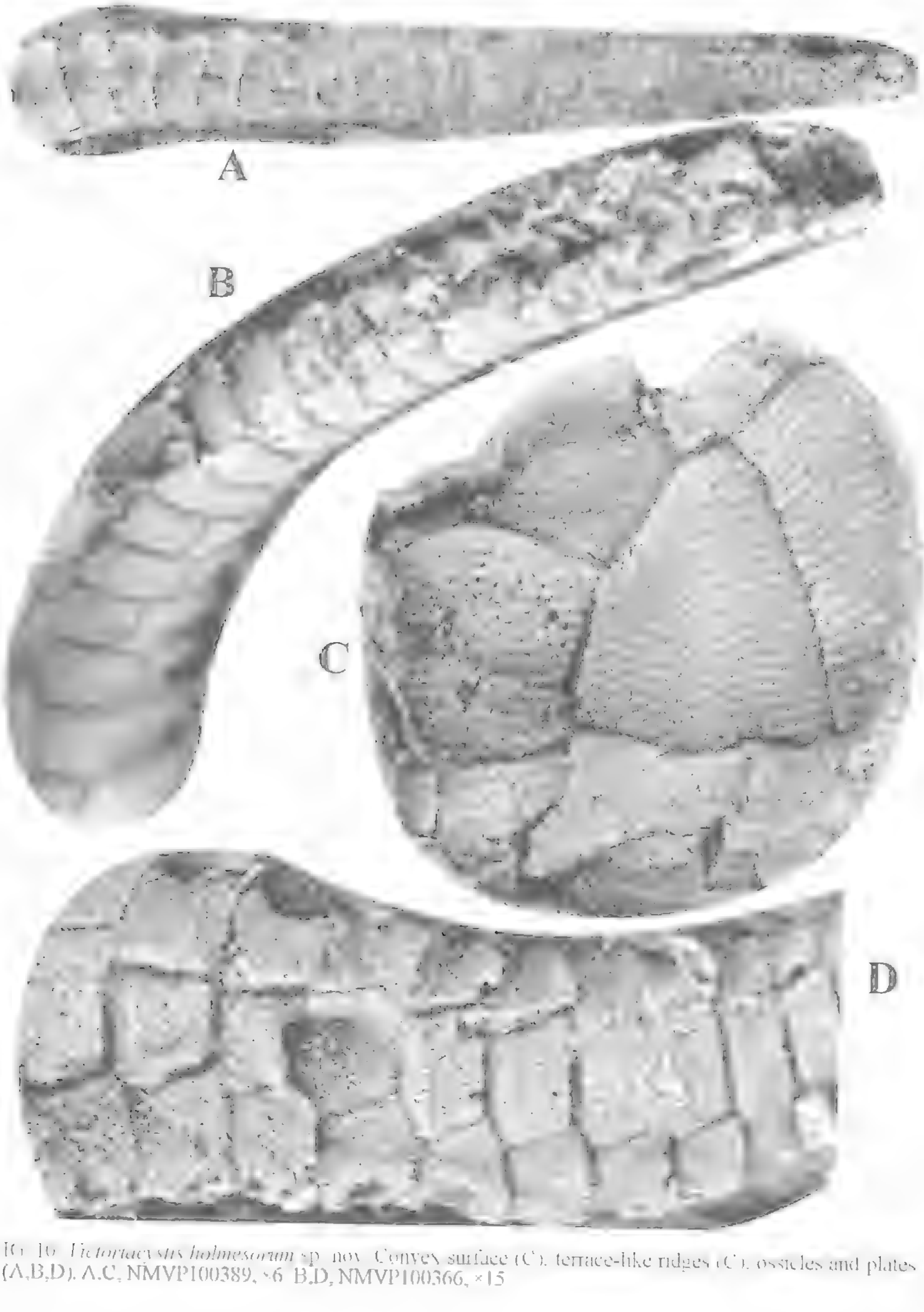


FIG. 16. *Victoriacystis holmesorum* sp. nov. Convex surface (C), terrace-like ridges (C), ossicles and plates (A,B,D). A,C, NMVP100389, ×6. B,D, NMVP100366, ×15.

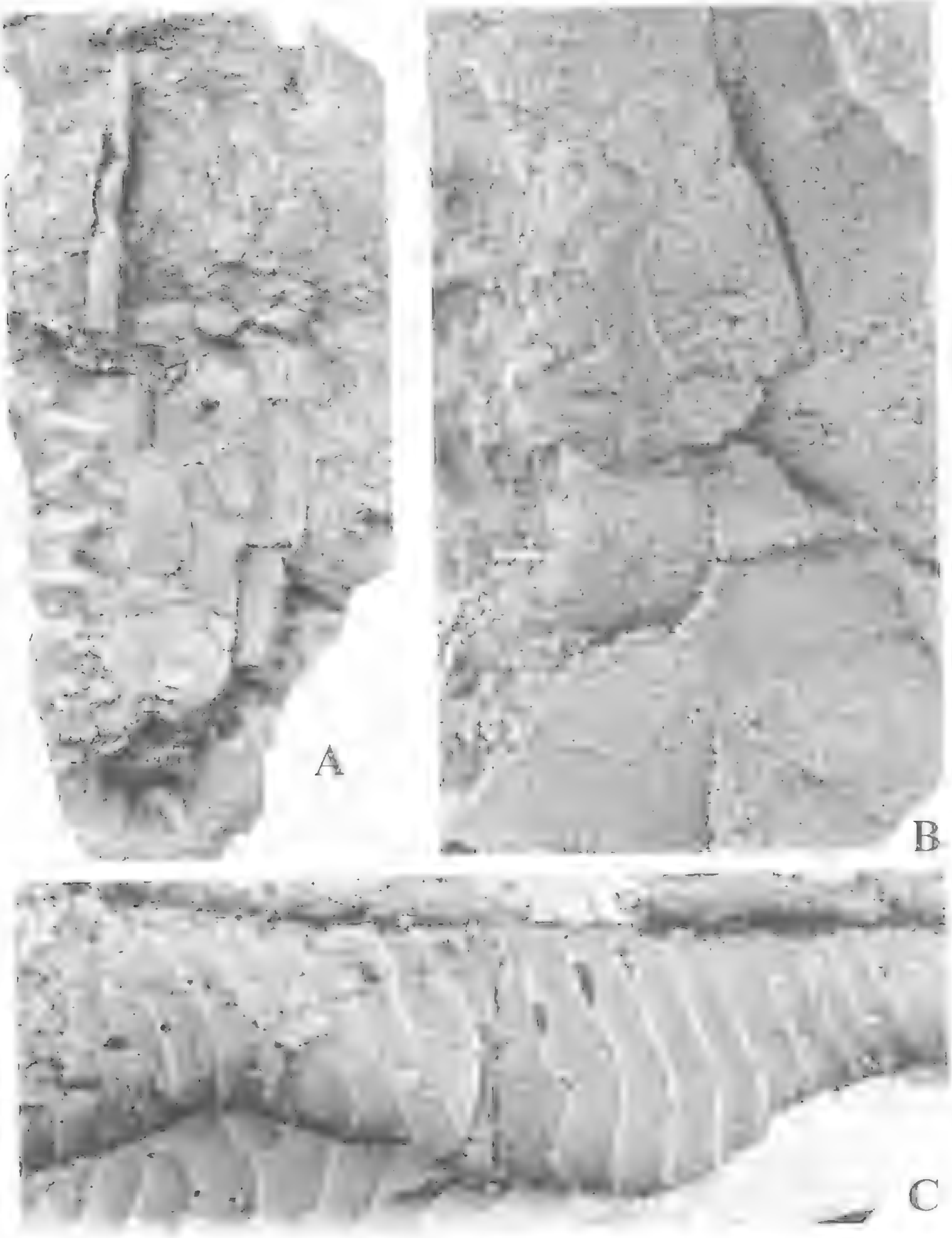


FIG. 11. *Victoriacystis holmesorum* sp. nov. Internal side of central part of convex surface (A, B) and transverse section of terrace-like ridges of plano-concave surface (C). A, B, NMVP100367, ×3 and ×12, respectively. C, NMVP108627, ×10.

with sharp lateral margin becoming more indistinct distally, with distal 1/3 circular or broadly elliptical in section (Figs 3A, 4A, 6A, 11A), with oblique gently convex, surrounded medially by slightly thickened margin and carrying low conical subcentral projection, giving insertion to toroidal process (Figs 2E, 3A, 5D, 6A, 7E). Right spines described individually: some (Fig. 3B-C) more slender, slightly shorter than left spine, uniformly decreasing in diameter proximo-distally, slightly flattened in proximal 1/2, with weak lateral keel, with proximal 1/4 separated from rest of the spine by abrupt geniculation; with distal 3/4 of spine straight or very gently curved medially; most others gently (Figs 2D-E, 3D-E, 5A-D, 6B-C, 7A-B) to strongly convex laterally (Figs 1A, 5C, 6D) proximally, laterally concave distally, forming a distinct distal hook in one specimen, with almost uniform cross-section proximo-distally and with blunt distal end, with articular surface similar to that of left spine, but perpendicular to main axis and without thickened medial margin.

INTERNAL. *Plano-concave surface.* Slightly oblique septum along left 1/2 of inside of C and of left PM, slightly sinuous in its distal 1/2, ending in poorly defined spur-like process subcentrally on distal 1/3 of C, with proximal part of septum convex laterally. Proximo-distally elongate, trough-like area of inside of left PM between septum and lateral margin of left PM. Faint ridge diverging laterally from the spur-like process, running on inside of C and right PM, flanking the lateral margin of the latter. Transverse ridge near distal margins of A and C, slightly concave distally, more robust on A, occupying almost the entire width of A, interrupted laterally on C. Proximal and distal surfaces of ridge sloping gently. Inside of other plates poorly preserved but apparently smooth.

*Convex surface.* Internal surface of C1-C5 margins slightly thickened (Fig. 5D), surrounded by very shallow peripheral groove, with distal 1/3 (Figs 5D, 7E) occupied by proximally recumbent walls at c.20° to internal surface of plates, extending almost completely across their width. Distal surfaces of transverse walls merging gradually into distal 1/3 of internal side of plates, also slightly raised with respect to their proximal 2/3. Walls on C1 and C5 c.1/2 as wide as walls on C2-C4, slightly thicker than these, torus-shaped with strongly convex, blunt free margin. Walls on C2-C4 rectangular, with straight, thinner free margin and with clear-cut separation of lateral margins from inside of plates. Internal surface of C6-C9 smooth and featureless. Subcentral, proximo-distally elongate thickening on internal surface of C10, C12 and C14. Lateral surfaces of thickenings almost vertical. Thickenings on C10 and C14 roughly elliptical, c. twice as long as wide. Thickening on C12 almost 3 times longer than wide, with subparallel lateral margins. Similar thickening, spindle-shaped in outline and with greater axis at c.60° to body axis, visible in the middle of plate C15 in NMVP100367 (Fig. 11A-B).

*Internal surface of C16* (Fig. 11A-B). Distal 1/2 not clear. Proximal 1/2 with a shallow cruciform area with irregular arms, outlined by thin ridges. Proximal arm short and stout, with gently concave margins, reaching proximo-lateral margin of C16. Distal margin of lateral arm curving distally as sinuous ridge joining lateral margin of distal arm of cross. Distal arm about twice as long as lateral and proximal arms.

APPENDAGE. 1-1.25 times body length; proximal part 3 times wider at proximal ring than at distal ring, with segments of proximal 1/3 of distal part decreasing in size and changing shape distally. Segments of central 1/3 of distal part decreasing uniformly in size and displaying less remarkable changes in shape. Distally appendage whip-like, with segments of approximately constant proportions.

*Proximal part.* Tetramerous rings with proximal one largest, with remainder of subequal length but decreasing width. Paired ring plates on plano-concave side, slightly smaller than those lying on opposite side, less convex in cross-section, with narrower thickening along distal margins (Figs 1A-B,E, 2A,D-E, 3D, 4A-B,F, 5B, 7B, 8A, 9A-C,E, 12A-C). Distal margin of proximal ring straight, without tubercles. Distal margins of other rings concave, with regularly spaced, subconical to hemispherical tubercles (Figs 1E, 2C-D, 3D, 4A-C, F, 5A-B, 8A, 9A-C,E). Articular surfaces on lateral ends of ring plates on same side as convex surface, proximo-distally elongate, triangular, with a subcentral, roughly circular shallow area (Figs 1B,E, 2C-D, 8A, 9A).

*Intermediate part.* Styloid (Figs 1B,E, 2D, 4B,F, 7A,C, 8A,B, 9A,E, 12A-B, 13B) robust. Proximal articular process just beneath proximal blade, subhorizontal, flattened, subtriangular. Proximal blade expanded transversely, recumbent, with free margin blunt, semicircular to broadly semielliptical. Narrow, sharp, median

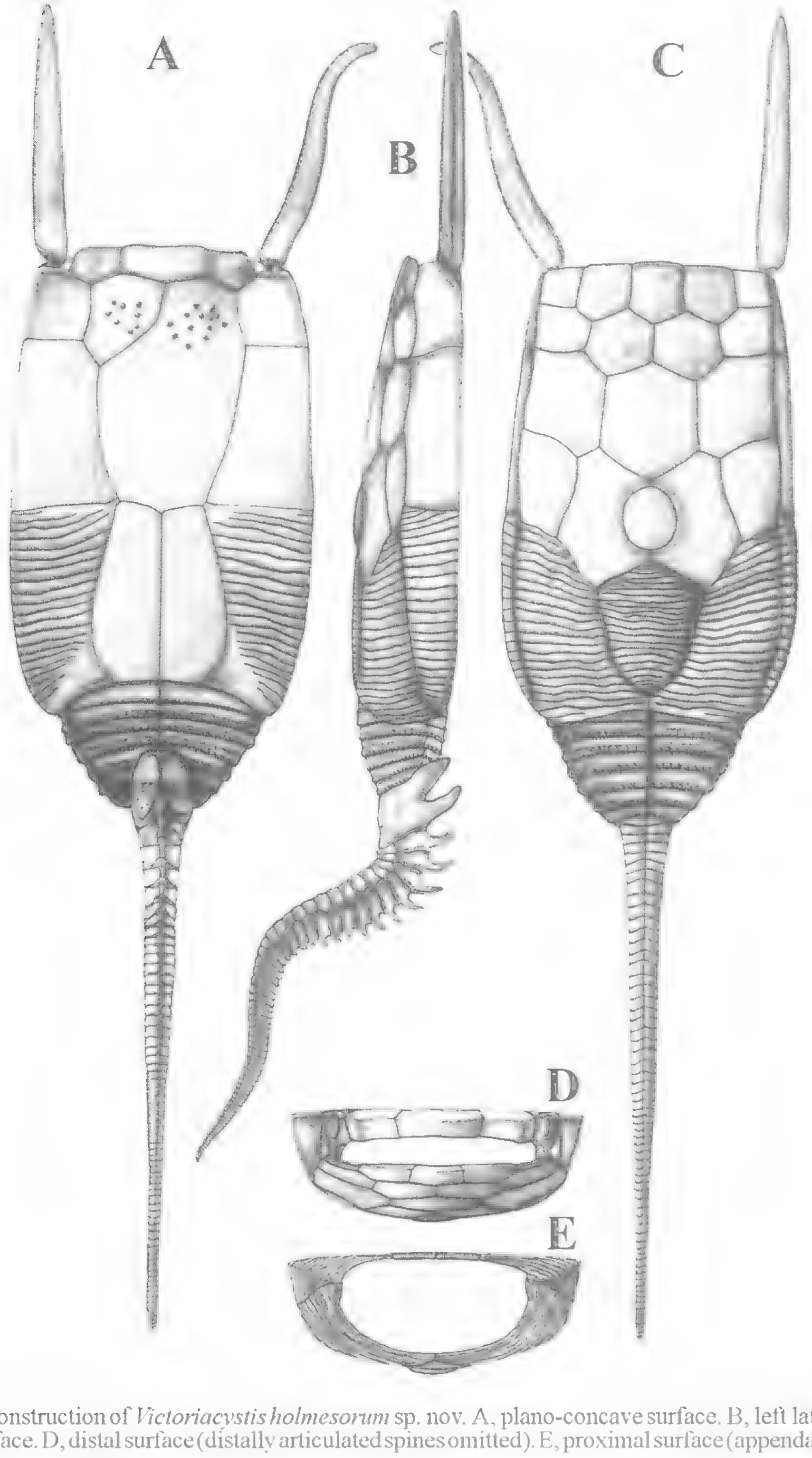


FIG. 12. Reconstruction of *Victoriacystis holmesorum* sp. nov. A, plano-concave surface. B, left lateral view. C. convex surface. D, distal surface (distally articulated spines omitted). E, proximal surface (appendage omitted).

longitudinal keel ending abruptly before reaching free margin of proximal blade and widening slightly in its distal 1/2. Region of blade facing proximally between free margin and insertion of proximal articular process vaulted. Distal blade 3 times as high as wide, spike-like. Proximal margin of distal blade narrowly acute but not sharp, slightly concave in lateral view in its lower 2/3 and almost straight in its upper 1/3 before merging into blunt blade apex. Lateral surfaces of distal blade flat to very gently concave in upper 2/3.

*Distal part*. (Figs 2B,D, 4B,F, 7A-C, 8B, 9A-E, 10A-B,D, 12A-C, 13A,C-D). Ossicles of first 5-6 segments slightly more than 3 times as high as long and divided into massive body and blade-like process, or apex. Processes of first 3 or 4 ossicles (Fig. 13A) almost as high as their bodies, gradually decreasing in height and length distally, wedge-shaped in transverse section, with strongly curved proximal margin. Proximal margins of processes merging into sharp median longitudinal keel with asymmetrical parabolic profile and occupying proximal 1/3 (in first 3 ossicles) to 1/2 (in subsequent 2 or 3 ossicles) of ossicular length. Articular margins for insertion of paired plates bearing smaller, shallower proximal facet and larger, deeper distal facet. Ossicles 7-9 (Fig. 10D) 3 times as high as long; processes narrower than on more proximal ossicles, decreasing in size distally, confined to distal 1/3-1/4 of ossicular length, subtriangular in lateral view. Keel slightly concave to straight in lateral view. Remaining ossicles (Figs 9B-D, 10A-B) subrectangular in lateral view, 3 times as high as long, with almost straight proximal and distal margins; processes diminishing distally, cuspate, shaped like an equilateral triangle in cross-section. Terminal ossicles without processes.

Proximal (Fig. 13C) and distal (Fig. 13D) articular surfaces parabolic, slightly taller than wide, comprising an outer interossicular depression, an inner interossicular depression and a median interossicular groove. Outer interossicular depression delimited laterally by slightly thickened ossicular margin of uniform width and medially by thinner, ascending ridges forming external subelliptical boundary of inner interossicular depression, becoming thinner and narrower apically. Inner interossicular depression elliptical, occupying most of apical 2/3 of articular surface. Internal boundary of depression delimited by faint vertical ridges flanking median interossicular groove. Abapical ends of ascending ridges turned abruptly laterally, merging into free, semicircular rims of 2 articulation bosses on proximal articular surface of ossicle. Ridges marking proximal margins of subtriangular facets for articulation with paired plates of preceding segment of distal part of appendage.

Distal articular surface of ossicles (Fig. 13D) differing from proximal articular surface in apically tapering median interossicular groove, comparatively deeper lateral regions of outer ossicular depression and trough-like, elongate articular pit delimited by 2 thick ridges diverging apically and laterally, occupying same position as articular bosses on outer ossicular depression.

Paired plates of distal part of appendage changing shape and size throughout appendage length (Figs 2D, 4B,F, 8B, 9A-C, 10A-B,D). Each plate articulating with distal facet of overlying ossicle and with proximal facet of next distal ossicle. First 4 pairs of plates at least twice as high as long, with gently convex distal margin, with sinuous to straight proximal margin. Subsequent 4 pairs of plates with decreasing height/length ratio almost as long as high. Remaining plates subsemicircular in lateral profile.

*Appendage stereom*. Stereom of proximal rings generally compact, especially along free margins of ring plates, or with small subcircular pores, resembling that of central surface area of body plates, often with small granulations distributed randomly, rarely with coarse trabeculae and irregular pores. Styloid stereom usually compact, rarely microperforate, sometimes with irregular, elongate trabeculae near margins of lateral surfaces of distal blade. External surface of plates and ossicles of distal part of appendage usually covered with regular, subcircular shallow pits separated by short trabeculae. Stereom near free margins of ossicles and plates generally more compact, with smaller pits and more irregular trabeculae, the latter sometimes elongate and giving rise to faint striations, especially near apex of ossicular processes.

DISCUSSION. *Victoriacystis holmesorum* closely resembles *V. wilkinsi* and *Rhenocystis latipedunculata* Dehm, 1932 especially in the number and arrangement of plates on the convex surface (Ruta, 1997, in press; Ruta & Bartels, 1998). *Rhenocystis* is distinguished from *Victoriacystis* by the plate arrangement of row II, in which C7 and C8 are separated by interposition of C3 and C12. *V. holmesorum* is larger and more robust than *V. wilkinsi* and *R. latipedunculata*. It

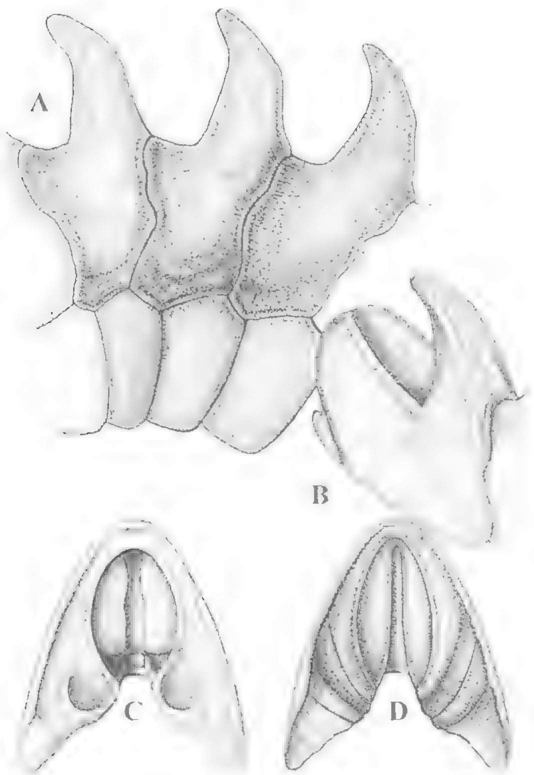


FIG. 13. Reconstruction of *Victoriacystis holmesorum* sp. nov. A, most proximal segments of distal part of appendage. B, styloid in left laterodistal view. C,D, proximal and distal articular surfaces of ossicle of intermediate region of distal part of appendage.

differs from *V. wilkinsi* in its differentiated distal part of the appendage, larger plates of row III, C10 C12 and C14, with respect to more proximal and distal elements, narrower proximal 1/2 of C16 and C18 with respect to distal 1/2, lack of contact between C17 and either proximal angle of C12 or distal angle of C21, larger A with respect to LOP and MOP, usually strongly arcuate or geniculate suture between A and C, more robust and larger styloid, more strongly recurved proximal ossicular blades, absence of tubercles from the paired plates of the distal part of the appendage and longer and more robust spines, sometimes with remarkably different morphology.

**Pseudovictoriacystis** gen. nov.

TYPE SPECIES. *Pseudovictoriacystis problematica* sp. nov.

ETYMOLOGY. Greek *pseudo*, false, plus *Victoriacystis*; alluding to resemblance between new genus and *Victoriacystis*. Feminine.

DIAGNOSIS. Distal 1/2 of convex surface of rows I and III, with 5 and 3 elements respectively. Distal margin of convex surface slightly convex centrally, concave laterally. C12 in contact with C2-C4. Lateral margins of C12 diverging slightly distally. C10 and C14 larger than C12, sutured with C1-C2 and with C4-C5, respectively. Proximal 1/2 of convex surface of rows IV and V, the former including C15, C17 and C19. C15 and C19 subtrapezoidal, their lateral margins 1.5 times as long as medial margins. C17 shield-shaped, at least 3 times as wide distally as proximally, with 3-lobed distal margin. C20 and C22 almost 1/2 as long as body, with strongly sinuous medial margins and very gently convex lateral margins. C21 narrowly inserted between C20 and C22, at least twice as long as wide, reaching maximum width in proximal 1/3.

**Pseudovictoriacystis problematica** sp. nov.
(Figs 14-16)

ETYMOLOGY. Greek *problema*, question; alluding to the puzzling plate configuration of the convex surface.

MATERIAL. HOLOTYPE: NMVP100383 from NMVPL252.

DIAGNOSIS. As for genus.

DESCRIPTION. Length 24mm, width 16mm, broadly rectangular. DLM and LOP of left side, C15, spines and articulated appendage not preserved.

*Plano-concave surface*. Plating pattern and general plate proportions similar to *Victoriacystis holmesorum*. Differences as follows (Figs 14A, 15A): maximum body width about halfway along PLM; lateral margins of ILM and DLM straight; shallower lateral body walls; much greater PLM/ILM length ratio; length of distal margin of PLM/length of proximal margin of PLM slightly lower; proximal 1/3 of lateral margins of PLM more strongly curved medially; distal margins of PLM sinuous, with medial 1/2 proximally convex and lateral 1/2 proximally concave; PM about as long as C; lateral margins of PM more gently convex and with most proximal part forming deep semicircular notch; proximo-lateral angles of PM extended as narrow lateral elongate processes; proximal margins of PLM and PM at obtuse angle rather than merging gradually; medial margins of ILM slightly more concave; DLM about twice as long as wide, with

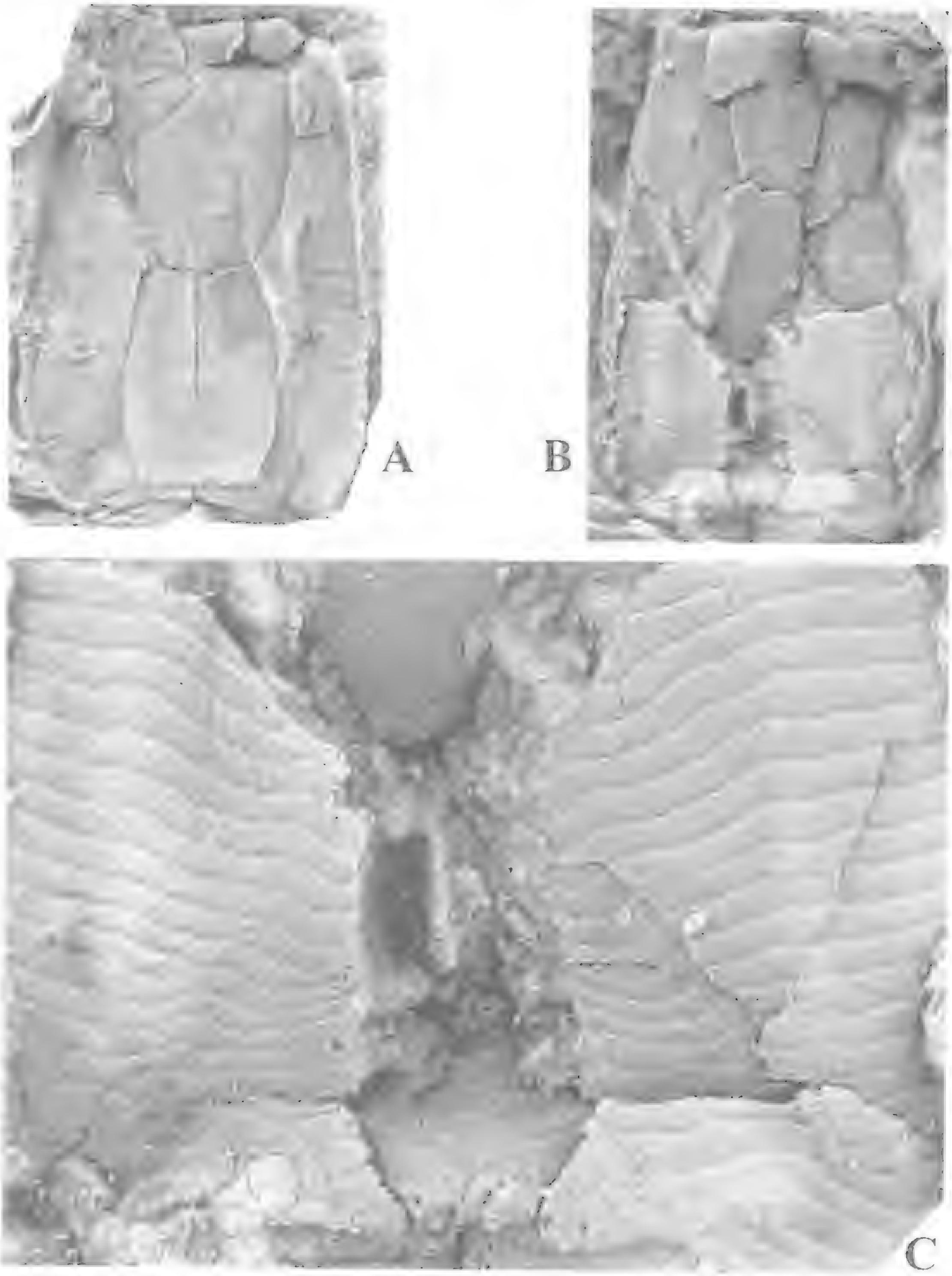

FIG. 14. *Pseudovictoriacystis problematica* gen. et sp. nov. Holotype, NMVP100383. A,B, plano-concave and convex surfaces, respectively, ×3. C, close-up of C20-C22, ×10.

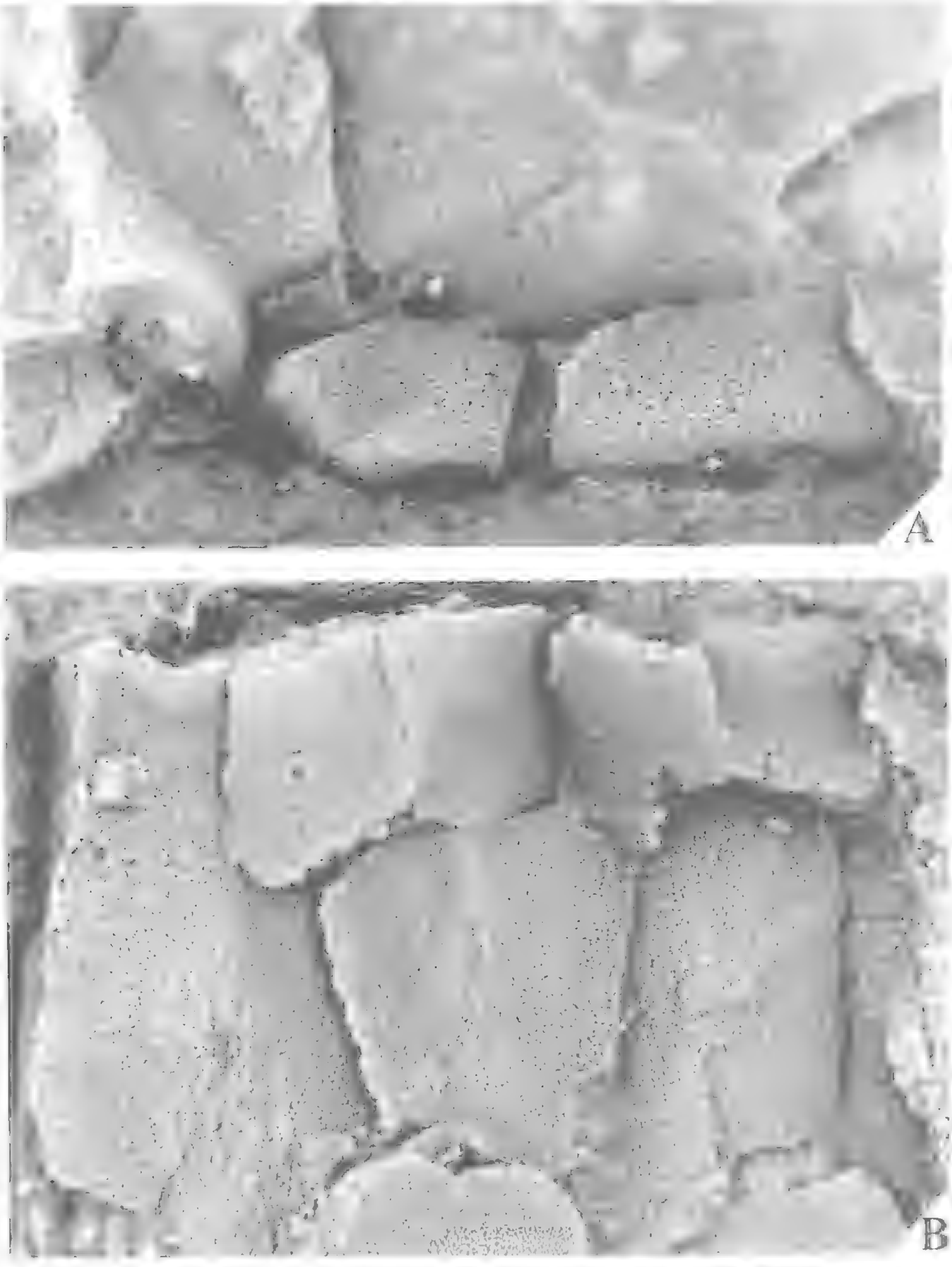


FIG. 15. *Pseudovictoriacystis problematica* gen. et sp. nov. Holotype, NMVP100383. A, close-up of right LOP, MOP and articular surface of right DLM, ×15. B, close-up of distal part of convex surface, ×10.

distally protruding articular region for spine insertion and shallow depressed area medial to articular region; distal surface of articular region teardrop-shaped, with lateral end forming an acute angle and divided into 2 distinct parts: lateral part broadly triangular and shallowly concave; medial part subcircular and markedly convex distally, bearing small, subcentral toroidal process giving rise to a short, faint medial and lateral ridge; suture between A and C mostly straight, at c.60° to longitudinal body axis, gently curved and meeting proximal margin of MOP in distal 1/4.

*Convex surface* (Figs 14B-C, 15B, 16). Slightly disrupted; proximal 1/2 reconstructed tentatively. Transverse rows of plates 4; distal row with 5 plates, homologous with C1-C5 of other anomalocystitids (e.g. *Rhenocystis* and *Victoriacystis*). C2 and C4 subtrapezoidal, with distally converging lateral and medial margins and with lateral 2/3 of proximal margins broadly convex and lying proximal to proximal margin of C3. C1 and C5 subrectangular, about twice as long as wide, with broadly concave distal margins. Row II of 3 plates (=C10, C12 and C14 based on shape and proportions). C10 and C14 longer than wide, subpentagonal, with medial angles strongly developed into points. C12 in contact with C3 medially and C2 and C4 laterally. Lateral margins of C12 mostly straight, slightly convex at proximal and distal ends. C15 and C19 smaller, subtrapezoidal, with convex margins. C17 with L/W ratio of 1.4, with lateral margins divided into sinuous distal 1/2 and distally diverging concave proximal 1/2, with distal margin broadly convex, with expanded central section. C20 and C22 with distal to proximal margins; distal margins <1/3 plate length, oriented slightly oblique to longitudinal axis, slightly concave; lateral margins very gently convex in distal 1/2, more strongly convex in proximal 1/2. Proximal margins merging into lateral margins, forming proximally protruding blunt-ended angles, with lateral 2/3 of proximal margins slightly convex, with medial 1/3 gently sinuous, forming central excavation into proximal margin. Medial margins convex but with smooth invagination distal to rounded medial projections at proximal end. C21 (Fig. 14B-C) trapezoidal, inserted between C20 and C22, with gently convex proximal margin, with 4-5 irregular ridges, with one bifurcated laterally.

*Sculpture*. PLM with robust terrace-like ridges, with thickened free margin; ridges irregularly sinuous, unevenly spaced, sometimes interrupted medially or giving rise to irregular lateral bifurcations, with most proximal ridges short and at c.45° to body axis, with smooth broadly trapezoidal area of external surface (Fig. 14A). Terrace-like ridges on C20 and C22 (Figs 14B-C) less steep than on PLM, without thickened free margin, oriented mainly transverse to longitudinal body axis but irregularly sinuous. Single, sigmoidal ridge at 45° to longitudinal axis on proximolateral 1/4 of external surface of C19.

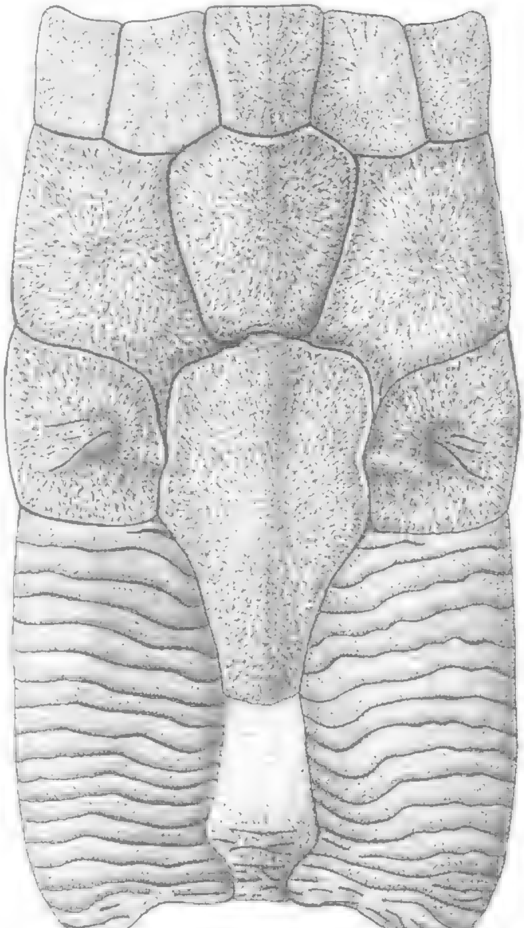

FIG. 16. Reconstruction of convex surface of *Pseudovictoriacystis problematica* gen. et sp. nov.

*Body stereom*. Stereom of plano-concave surface similar to that of *Victoriacystis holmesorum*, but consisting of slightly coarser meshwork, especially in the centres of the plates, often forming a reticulate pattern of irregular pores and trabeculae. Peripheral surface, especially on A, C, MOP and ILM, with elongate pores and thin, straight trabeculae arranged radially (Figs 14A,

15A). Stereom of convex surface retiform except on C20-C22 (Fig. 15B-C). All other plates, but especially those of the 2 most distal transverse rows, with distinct surface pattern with pores increasing in size, becoming more elongate and arranged more regularly from centre to margins of plates, separated by radiating trabeculae, often dichotomously branching towards the periphery. Pores near plate margins polygonal, separated by short trabeculae, giving rise to coarse, cancellate surface pattern of stereom. Stereom of periphery of C17 and of medial 1/2 of C19 of densely spaced, circular to subelliptical pores, without obvious radiating arrangement of trabeculae.

REMARKS. The possibility that NMVP100383 is a teratological individual of *Victoriacystis holmesorum* cannot be entirely ruled out. It closely resembles the latter in plating of the plano-concave surface. Although rare, pathological mitrate specimens are known (Ruta, 1998). However, in all known cases, abnormal individuals can be assigned to known species, based on their possession of most of the characters shared with normal individuals.

Pending discovery of additional specimens to confirm diagnostic features, NMVP100383 is here placed in a new taxon because the configuration of its convex surface reveals a unique combination of attributes not observed in any other species.

Plate arrangement of distal 1/2 of convex surface resembles that of *Placocystites forbesianus* de Koninck, 1869 (Jefferies & Lewis, 1978) from the English Wenlock. In *Pseudovictoriacystis* and in *Placocystites*, C10, C12 and C14 are sutured with row I, there is no intervening row II and C12 is slightly smaller than both C10 and C14. *Pseudovictoriacystis* differs from *Placocystites* in being much longer than wide, in displaying a more limited distribution of terrace-like ridges, in possessing 5 rather than 3 plates in row I and in showing a much simpler plate configuration on proximal 1/2 of convex surface, apparently without plates C16 and C18 and with enlarged C17. Furthermore, C3 is separated from C10 and C14 by interposition of C2 and C4 and appears to be comparable in size with C1 and C5 and slightly smaller than C2 and C4.

The much older *Kopficystis kirkfieldi* Parsley, 1991 from the Trentonian of Ontario, vaguely resembles *Pseudovictoriacystis* in its 3-plated transverse row on distal 1/2 of convex surface. However, identification of the skeletal plates in that taxon is problematic (Ruta, in press). Unlike *Pseudovictoriacystis, Kopficystis* has 5 rather than 4 transverse rows of plates. Assuming the correctness of plate homologies discussed by Parsley (1991) and Ruta (in press), the most distal skeletal elements in this anomalocystitid correspond to C1, C6, C9, C10, C12 and C14 and to CM1, o, j, gl, i and e respectively in the terminology of Parsley (1991).

Although *Pseudovictoriacystis* displays a unique set of skeletal features, it is impossible to ascertain its affinities; we regard this form as deriving from a *Victoriacystis*-like ancestor.

## ACKNOWLEDGEMENTS

We thank David Holloway (Museum of Victoria), Steve Eckardt and Frank and Enid Holmes for help in the field. M.R. is grateful to the Queensland Museum (Brisbane) for generous hospitality and for the use of facilities. A.R. Milner (Birkbeck College, University of London), R.P.S. Jefferies, A.C. Milner, S.J. Culver and L.R.M. Cocks (Natural History Museum, London) read a draft of the manuscript. P. Crabb (Natural History Museum, London) photographed the specimens. We thank Dennis Kolata and Colin Sumrall for useful reviews but the views expressed herein are those of the authors alone. This work was carried out while M.R. was in receipt of a European Community grant (Training and Mobility of Researchers).

## LITERATURE CITED

CASTER, K.E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology 34: 1-47.

CASTER, K.E. & GILL, E.D. 1967. Family Allanicytidiidae, new family. Pp. S561-S564. In Moore, R.C. (ed.) Treatise on invertebrate paleontology, Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas : New York).

DEHM, R. 1932. Cystoideen aus dem rheinischen Unterdevons. Neues Jahrbuch für Mineralogie, Geologie und Paléontologie, Beilage-Band, Abteilung A 9: 63-93.

GILL, E.D. 1948. A new trilobite from the Yeringian (Lower Devonian) rocks of Kinglake, Victoria. Proceedings of the Royal Society of Victoria 59: 8-19.

GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology 41: 5-71.

HOLLOWAY, D.J. & JELL, P.A. 1983. Silurian and Devonian edrioasteroids from Australia. Journal of Paleontology 57: 1001-1016.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3: 1-128.

JEFFERIES, R.P.S. 1968. The Subphylum Calcichordata (Jefferies 1967) – primitive fossil chordates with echinoderm affinities. Bulletin of the British Museum (Natural History), Geology Series 16: 243-339.

1990. The solute *Dendrocystoides scoticus* from the Upper Ordovician of Scotland and the ancestry of chordates and echinoderms. Palaeontology 33: 631-679.

JEFFERIES, R.P.S. & LEWIS, D.N. 1978. The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. Philosophical Transactions of the Royal Society of London, Series B 282: 205-323.

JELL, P.A. 1983. Early Devonian echinoderms from Victoria (Rhombifera, Blastoidea and Ophiocistioidea). Memoirs of the Association of Australasian Palaeontologists 1: 209-235.

KOLATA, D.R. & JOLLIE, M. 1982. Anomalocystitid mitrates (Stylophora, Echinodermata) from the Champlainian (Middle Ordovician) Guttenberg Formation of the Upper Mississippi Valley Region. Journal of Paleontology 56: 531-565.

KONINCK, M.L. de 1869. Sur quelques échinodermes remarquables des terrains paléozoiques. Bulletin de l'Académie Royale des Sciences Belgique 28: 544-552.

PARSLEY, R.L. 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). Bulletins of American Paleontology 100: 5-57.

RUTA, M. 1997. Redescription of the Australian mitrate *Victoriacystis* with comments on its functional morphology. Alcheringa 21: 81-101.

1998. An abnormal specimen of the Silurian anomalocystitid mitrate *Placocystites forbesianus*. Palaeontology 41: 173-182.

In press. A cladistic analysis of the anomalocystitid mitrates. The Zoological Journal of the Linnean Society.

RUTA, M. & BARTELS, C. 1998. A redescription of the anomalocystitid mitrate *Rhenocystis latipedunculata* from the Lower Devonian of Germany. Palaeontology 41: 771-806.

RUTA, M. & JELL, P. A. 1999a. *Adoketocarpus* gen. nov., a mitrate from the Ludlovian Kilmore Siltstone and Lochkovian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 377-398.

1999b. A note on *Victoriacystis wilkinsi* (Anomalocystitida: Mitrata) from the Upper Silurian of Victoria. Memoirs of the Queensland Museum 43: 423-430.

RUTA, M. & THERON, J.N. 1997. Two Devonian mitrates from South Africa. Palaeontology 40: 201-243.

STRUSZ, D.L. 1972. Correlation of the Lower Devonian rocks of Australasia. Journal of the Geological Society of Australia 18: 427-455.

TALENT, J.A. 1967. Silurian sedimentary petrology and palaeontology. Bulletin of the Geological Survey of Victoria 59: 24-29.

UBAGHS, G. 1967. Stylophora. Pp. 496-565. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York).

1969. Les échinodermes carpoides de l'Ordovicien inférieur de la Montagne Noire (France). Cahiers de Paléontologie. (Éditions du Centre National de la Recherche Scientifique: Paris).

VANDENBERG, A.H.M. 1988. Silurian-Middle Devonian. Pp. 103-146. In Douglas, J.G. & Ferguson, J.A. (eds) Geology of Victoria. (Victorian Division of the Geological Society of Australia: Melbourne).

VANDENBERG, A.H.M, GARRATT, M.J. & SPENCER-JONES, D. 1976. Silurian-Middle Devonian. Special Publications of the Geological Society of Australia 5: 45-76.

WILLIAMS, G.E. 1964. The geology of the Kinglake district, central Victoria. Proceedings of the Royal Society of Victoria 77: 273-328.

WOODS, I.S. & JEFFERIES, R.P.S. 1992. A new stem-group chordate from the Lower Ordovician of South Wales, and the problem of locomotion in boot-shaped cornutes. Palaeontology 35: 1-25.

# A NOTE ON *VICTORIACYSTIS WILKINSI* (ANOMALOCYSTITIDA: MITRATA) FROM THE UPPER SILURIAN OF VICTORIA

MARCELLO RUTA AND PETER A. JELL

Ruta, M. & Jell, P.A. 1999 06 30: A note on *Victoriacystis wilkinsi* (Anomalocystitida: Mitrata) from the Upper Silurian of Victoria. *Memoirs of the Queensland Museum* **43**(1): 423-430. Brisbane. ISSN 0079-8835.

New material of *Victoriacystis wilkinsi* from the Upper Silurian of Victoria reveals new features of the convex surface and permits a more detailed comparison with the congeneric *V. holmesorum* from the Lower Devonian. A revised diagnosis is provided for *V. wilkinsi*, together with a description of the best preserved among the new specimens. ☐ *Anomalocystitida, Victoriacystis, Silurian, Victoria.*

*Marcello Ruta, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom; Peter A. Jell, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia;* *received 2 July 1998.*

Subsequent to the redescription of the Ludlow anomalocystitid *Victoriacystis wilkinsi* Gill & Caster, 1960 from the Dargile Formation, Heathcote and Melbourne Formation, Hawthorn (Ruta, 1997), we examined additional material in the Museum of Victoria, Melbourne, part of which extends the known distribution of this species. New specimens are generally more complete and fully articulated than those figured by Gill & Caster (1960) and Ruta (1997) and clarify details of the external and internal anatomy of this mitrate. Major differences between *V. wilkinsi* and *V. holmesorum* Ruta & Jell, 1999 from the Lower Devonian Humevale Formation of central Victoria were highlighted by Ruta & Jell (1999b).

## SYSTEMATIC PALAEONTOLOGY

Terminology and plate nomenclature are as used elsewhere in this volume (Ruta & Jell, 1999a). All material is housed in the Museum of Victoria Palaeontological Collections (NMVP) and localities entered in the fossil locality register of the same Museum (NMVPL). All illustrations are of latex casts from internal and external moulds whitened with ammonium chloride sublimate unless otherwise stated.

Class STYLOPHORA Gill & Caster, 1960
Order MITRATA Jaekel, 1918
Suborder ANOMALOCYSTITIDA Caster, 1952
Family PLACOCYSTITIDAE Caster, 1952

DIAGNOSIS. Lateral margins of PM convex for most of their length. C3 and C12 in contact with each other. Proximo-lateral angles of C3 truncated (condition of second and third characters reversed in *Victoriacystis*) (Caster, 1952; Parsley, 1991; Ruta & Jell, 1999b; Ruta, in press).

### **Victoriacystis** Gill & Caster, 1960

TYPE SPECIES. *Victoriacystis wilkinsi* Gill & Caster, 1960 from the Ludlow Dargile Formation, Victoria.

DIAGNOSIS. See Ruta & Jell (1999b) and Ruta (in press).

OTHER SPECIES. *Victoriacystis holmesorum* Ruta & Jell, 1999b from the Lochkovian of the Humevale Formation, central Victoria.

### **Victoriacystis wilkinsi** Gill & Caster, 1960 (Figs 1-5)

MATERIAL. NMVP23086, 109203 from F41-42 (type locality of Gill & Caster, 1960) (Dargile Fm: Ludlow). NMVP18313-18317 from City Brick Co. pit, Camberwell Rd, Hawthorn (Gill & Caster, 1960) (Melbourne Fm: Ludlow). NMVP22160-22161, 22348, 24111, 100457-100458, 100461-100462, 100464-100468 from NMVPL299 (= F31 of Williams, 1964) road cutting S of Bald Hills, 3.2km E of Kilmore (Dargile Fm: Ludlow). NMVP100446-100448 from NMVPL300 (= X64 of Williams, 1964) vicinity of disused mine on Comet Creek, 4.6km SE of Clonbinane (Humevale Fm: Ludlow). NMVP149352 from NMVPL1927 on Broadhurst Creek at the crossing of the Kilmore to Wandong Rd (see Vandenberg, 1992) (Kilmore Siltstone: Ludlow).

DIAGNOSIS (see also Ruta & Jell (1999b) and Ruta (1997, in press)). Lateral body walls slightly diverging ventrally. C-ILM sutures straight, convex or, rarely, sinuous. A-C suture straight or slightly geniculate, at <40° to body axis. PLM much wider distally than proximally. Medial

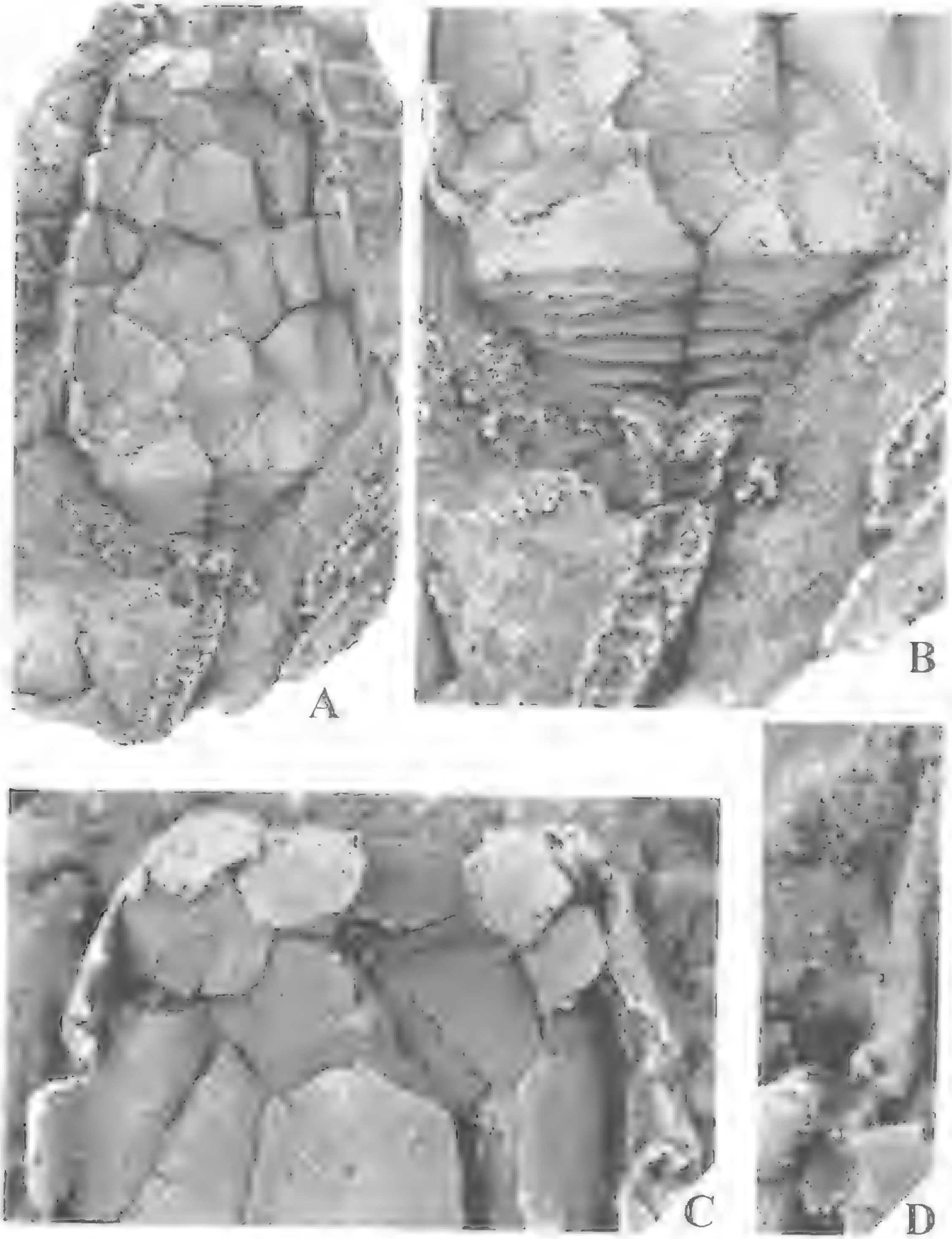


FIG. 1. *Victoriacystis wilkinsi* Gill & Caster from NMVPL300. A-C, convex surface, detail of proximal part of appendage and detail of distal part of inside of A, respectively, of NMVP100447, ×3, ×6 and ×8, respectively. D, detail of right spine from Fig. 2C, NMVP100448, ×8.

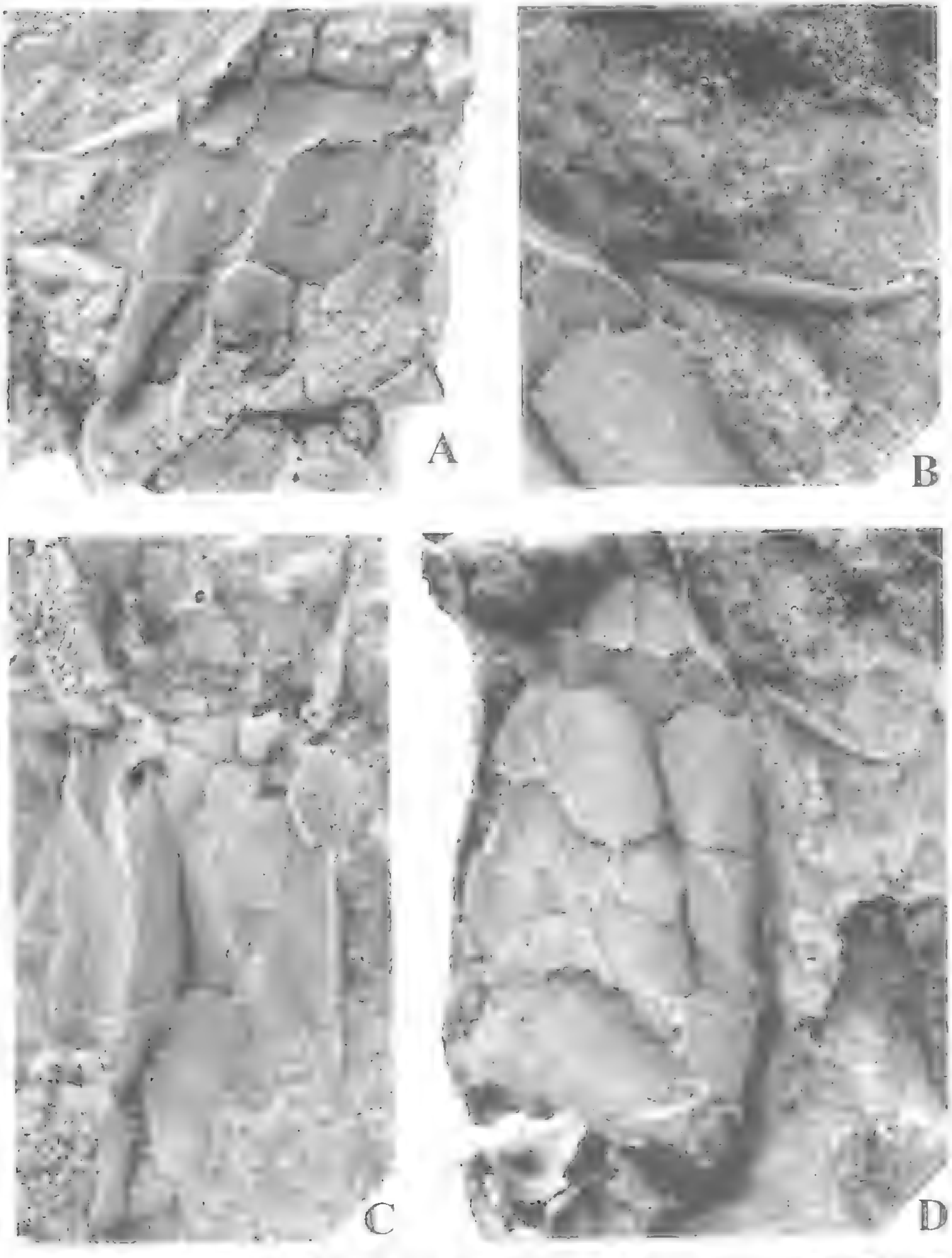

FIG. 2. *Victoriacystis wilkinsi* Gill & Caster. A-B, D, inside of convex surface, detail of left spine and convex surface, respectively, of NMVP100462, from NMVPL229, ×5, ×8 and ×5, respectively; C, plano-concave surface of NMVP100448 from NMVPL300, ×4.

margins of DLM straight. Proximal margins of PM occupying >1/2 proximal body excavation. Rows II-IV perpendicular to longitudinal axis or only gently concave distally. C10, C12 and C14 only slightly larger than C16 and C18. Sutures between C15 and C16 and between C18 and C19 strongly diverging proximally. C16 and C18 longer and wider than C15 and C19. C3 much larger than C2 or C4. Few, widely spaced ridges on proximal 1/2-1/3 of C16 and C18 and near lateral margins of PM. Spout-shaped thickenings internally on C2-C4. Tetramerous rings with weak distal thickenings lacking knobs. Styloid with slightly recurved, poorly developed distal blade only slightly higher than proximal blade. Distal part of appendage not differentiated. Distal ossicles with straight to gently concave distal margins, poorly developed ossicular apices and markedly sloping apical margins.

DESCRIPTION. EXTERNAL. We describe those features not reported by Gill & Caster (1960) or Ruta (1997). Body outline sometimes vase-shaped, with maximum width halfway along length of PLM. LOP subtrapezoidal to subpentagonal. MOP subrectangular, markedly asymmetrical. Distal margins of C2-C5 slightly distal to distal margins of LOP and MOP. Proximal margin of C17 sometimes accommodated by shallow notch on distal angle of C21 (Figs 1A, 2D, 3E). C21 otherwise shield-shaped (Fig. 1A), with geniculate lateral margins. Spines c. 1/3 as long as body, uniformly tapering distally, with blunt medial and lateral margins, with proximal 1/4 shaped like a truncated cone, with central shaft straight and slightly depressed, with distal 1/3 gently curved medially (Figs 1D, 2A-D, 3D). Terrace-like ridges often irregular and branched near proximolateral angles of plano-concave and convex surfaces (Figs 3E, 4E), irregularly sinuous and widely spaced on proximal 1/2 of C16 and C18.

INTERNAL. Septum on inside of plano-concave surface (Figs 3E, 4A); distal 1/2 of septum on interior of C straight and almost parallel to longitudinal axis, widening slightly halfway along its proximal part immediately lateral to the medio-distal angle of left PM. Septum becoming much shallower and broader beyond this point, giving rise to vaguely L-shaped structure straddling the triple junction formed by C with the 2 PM plates, deepening again and gently convex laterally on the lateral 1/2 of left PM. Cross-section of septum more asymmetrical (steeper to right) at PM than at C. Most distal part of C portion, corresponding to the diminutive spur of Ubaghs (1967), thickened and bent abruptly to the right at c. 30° to longitudinal axis. Most proximal part of septum on left PM not visible. Distal part of diminutive spur terminating abruptly. Rest of plano-concave surface almost featureless except for poorly pronounced ridge parallel to medio-distal margin of A, fainter medially than in its lateral 1/2, continuing on C along straight course, almost perpendicular to longitudinal axis and stopping abruptly before reaching lateral margin of C (Figs 1A,C, 4A).

Inside of convex surface (Fig. 2A) with button-like projections on C12, C14, C18 and C19, spout-shaped thickenings on C2, C3 and C4 and tortuous ridges on C16 and C18. Button-like projections only slightly raised with respect to surrounding plate surface, gently merging into the latter and slightly longer than wide; greater axis of projections on C14 and C19 at acute angle with longitudinal body axis. C12 projection slightly larger than remaining projections, c. 1/2 as large as C19 projection. Spout-shaped projections on C2, C3 and C4 (Figs 2A, 4B) of approximately equal size, occupying distal 1/3 of inside of plates, c. 1/3 as wide as these, delimiting a central and 2 lateral depressions, continuing distally into flat, sloping, rectangular area, and proximally into flat or gently convex trapezoidal area. Free margins of spout-shaped projections blunt, continuing laterally into narrow, transversely arched, vertical septa with sharp free margins. Ridges on C16 and C18 poorly preserved (Fig. 2A), apparently interrupted in places, with irregularly sinuous course.

APPENDAGE. Tetramerous rings 7-8, telescopic, with poorly developed distal thickenings without tubercles and blunt parasagittal section, with ring plates on the same side as convex surface of body showing gently convex distal margins (Figs 1A-B, 3A, D-E, 4A, D-E, 5A-E). Two distalmost ring plates on the same side as plano-concave surface of body slightly bent proximally, wrapped around proximal styloid process. Most distal ring plates lying on the same side as convex surface much smaller than more proximal plates, flanking the most proximal part of the styloid body immediately underneath free margin of proximal blade. Free margins of distal blade slightly concave proximally in lateral view, especially in abapical 1/2. Keel between proximal and distal blade sharp, with wedge-shaped lateral profile (Fig. 5A, C-D). Ossicles scarcely overlapping each other proximo-distally, with gently concave to

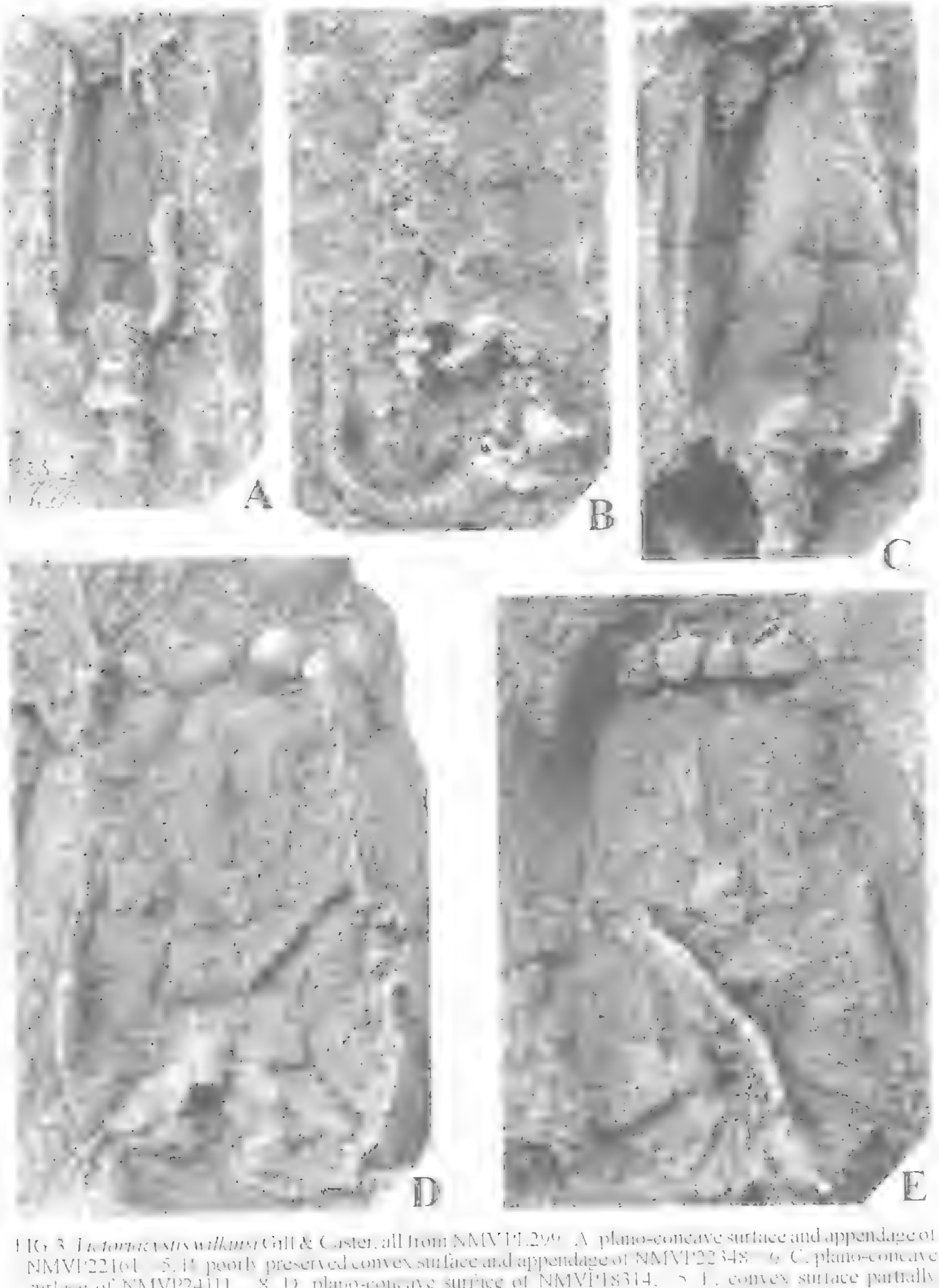


FIG. 3. *Victoriacystis wilkinsi* Gill & Caster, all from NMVPL299. A, plano-concave surface and appendage of NMVP22161, ×5. B, poorly preserved convex surface and appendage of NMVP22348, ×6. C, plano-concave surface of NMVP24111, ×8. D, plano-concave surface of NMVP18314, ×5. E, convex surface partially disarticulated and revealing distal half of inside of plano-concave surface of NMVP18316, ×5

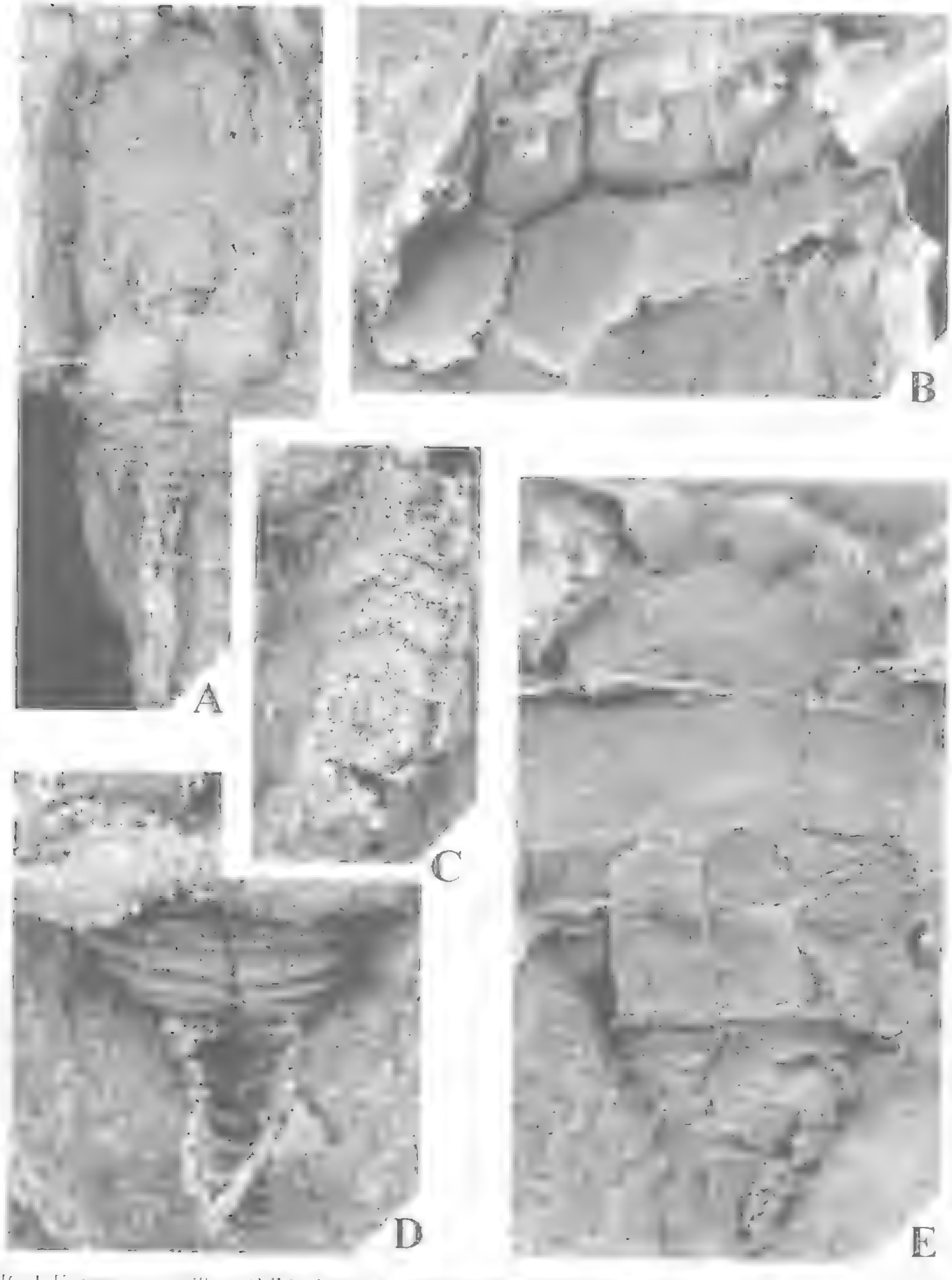


FIG. 4. *Victoriacystis wilkinsi* Gill & Caster. A, inside of plano-concave and part of exterior of convex surface of NMVP100446 from NMVPL300, ×3. B, interior of distal part of convex surface of NMVP100462, ×10. C, detail of distal part of appendage of NMVP100457, ×10. D, tetramerous rings of proximal appendage and interior of distal appendage of NMVP23086, ×8. B-D from NMVPL290. E, plano-concave surface of NMVP149352, from NMVPL1927, ×5.

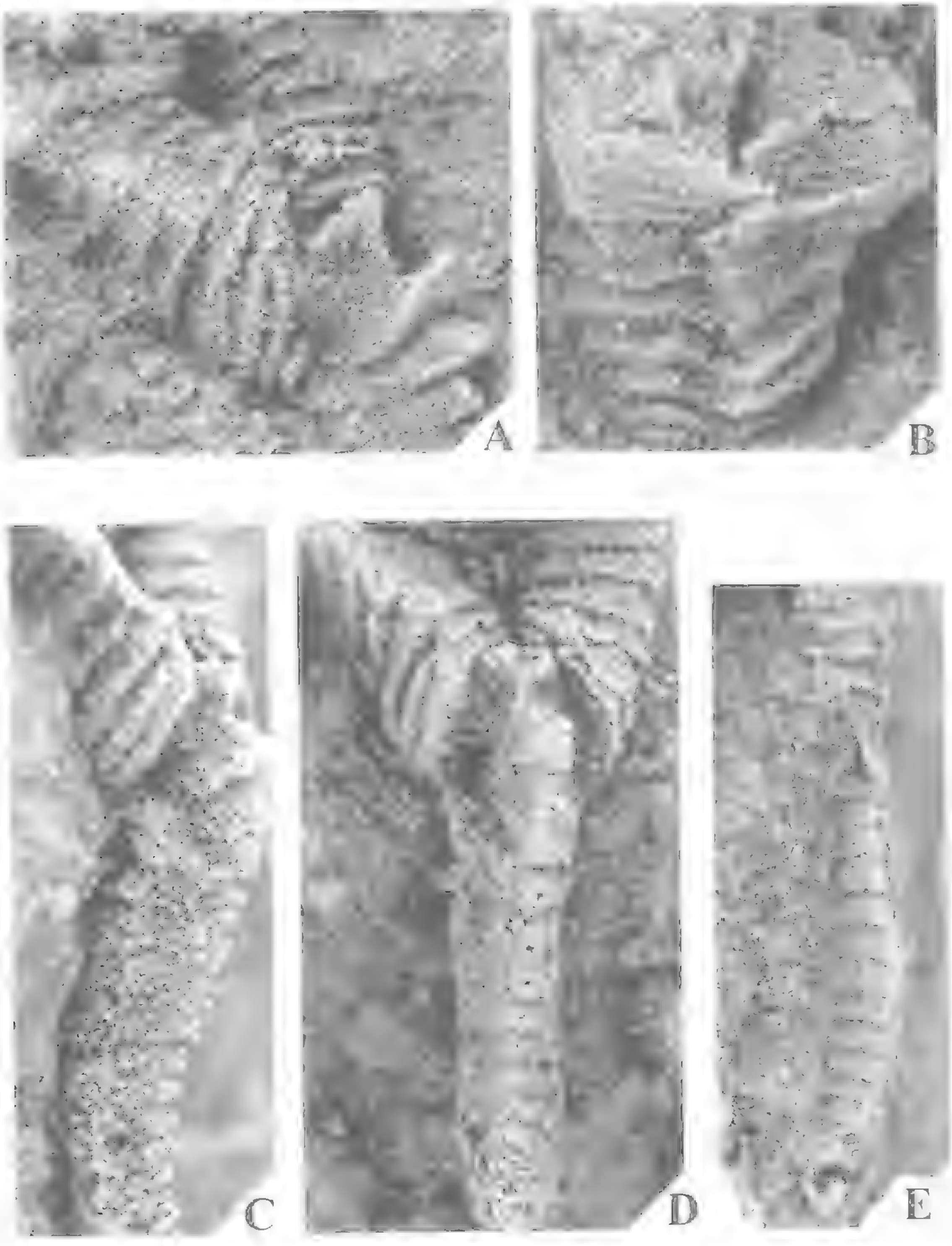


FIG. 5. *Victoriacystis wilkinsi* Gill & Caster. A-D from NMVPL299. Tetramerous rings, styloid, ossicles and paired plates. A, NMVP100457, ×10. B-D, NMVP100466, all ×8. E, NMVP100446 from NMVPL300, ×6.

almost straight distal margins, poorly pronounced apices and blunt, markedly sloping apical margins.

REMARKS. New specimens of *V. wilkinsi* show that the range of variation in several anatomical features (e.g. body outline; shape of LOP and MOP; proportions of C21) is broader than previously reported (e.g. Ruta, 1997). None of the new specimens shows the knobbly sculpture reported by Ruta (1997) on plate MOP. It is, therefore, impossible to establish whether such a sculpture is a genuine feature of this anomalocystitid. NMVP100462 (Figs 2A-B,D, 4B) provides the most complete information available on the inside of the convex surface. Internal characters of this surface are readily comparable with those of the congeneric *V. holmesorum* (Ruta & Jell, 1999b), although the 2 species differ in the shape of the internal thickenings on C2-C4. Several skeletal features show consistent variations in the 2 species of *Victoriacystis* (Ruta & Jell, 1999b) and new specimens of *V. wilkinsi* confirm this. Important differences are observed at the level of spines, and position, shape and proportions of several plates of the body and appendage.

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## LITERATURE CITED

CASTER, K.E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology 34: 1-47.

GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology 41: 5-71.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3: 1-128.

PARSLEY, R.L. 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). Bulletins of American Paleontology 100: 5-57.

RUTA, M. 1997. Redescription of the Australian mitrate *Victoriacystis* with comments on its functional morphology. Alcheringa 21: 81-101.

In press. A cladistic analysis of the anomalocystitid mitrates. Zoological Journal of the Linnean Society.

RUTA, M. & JELL, P.A. 1999a. *Adoketocarpus* gen. nov., a mitrate from the Ludlovian Kilmore Siltstone and Lochkovian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 377-398.

1999b. Two new anomalocystitid mitrates from the Lower Devonian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 399-422.

UBAGHS, G. 1967. Stylophora. Pp. 496-565. In Moore, R.C. (Ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York).

VANDENBERG, A.H.M. 1992. Kilmore 1:50,000 map and geological report. Geological Survey of Victoria Report 91: 1-86, + map.

WILLIAMS, G.E. 1964. The geology of the Kinglake district, central Victoria. Proceedings of the Royal Society of Victoria 77: 273-328.

# REVISION OF SILURIAN AND DEVONIAN ALLANICYTIDIIDAE (ANOMALOCYSTITIDA: MITRATA) FROM SOUTHEASTERN AUSTRALIA, TASMANIA AND NEW ZEALAND

MARCELLO RUTA AND PETER A. JELL

Ruta, M. & Jell, P. A. 1999 06 30: Revision of Silurian and Devonian Allanicytidiidae (Anomalocystitida: Mitrata) from southeastern Australia, Tasmania and New Zealand. *Memoirs of the Queensland Museum* **43**(1): 431-451. Brisbane. ISSN 0079-8835.

Additional specimens of the allanicytidiid anomalocystitids *Notocarpos garratti* (Upper Silurian, Victoria), *Tasmanicytidium burretti* (Lower Silurian, Tasmania) and *Allanicytidium flemingi* (Lower Devonian, New Zealand) yield new information, allowing revised diagnoses. *N. garratti* has a system of ridges on the internal surface of C20-C22 and a row of orifice platelets along distal transverse thickening on inside of C1 and C5. Internal ridges on C21 are homologous with similar structures in *Allanicytidium* and *Placocystella*. *T. burretti* has orifice platelets, faint ridges internally on C21, tetramerous rings proximally in the appendage and sculpture on the distal styloid blade. New material of *A. flemingi* shows external sculpture and stereom texture of convex surface, shape of C21 and proximal body excavation. ☐ *Allanicytidiidae, Silurian, Devonian, Victoria, Tasmania, New Zealand.*

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Despite extensive discussion on the interrelationships of allanicytidiid anomalocystitids (Caster & Gill, 1967; Philip, 1981; Caster, 1983; Haude, 1995; Ruta & Theron, 1997; Ruta & Jell, 1999a; Ruta, in press), numerous features of several species remain obscure or misinterpreted. All species except for the 2 most basal allanicytidiids, *Protocytidium elliottae* Ruta & Jell, 1999a from the Upper Ordovician of Victoria and *Occultocystis koeneni* Haude, 1995 from the Lower Devonian of Argentina, display very similar plate configurations, especially on the convex surface, making specific recognition difficult. Differences in external sculpture, in body proportions and in shape of individual plates provide diagnostic features (Ruta & Theron, 1997; Ruta, in press).

Newly available material of the allanicytidiids *Notocarpos garratti* Philip, 1981, *Tasmanicytidium burretti* Caster, 1983 and *Allanicytidium flemingi* Caster & Gill, 1967 clarifies poorly understood aspects of their anatomy, permitting revised diagnoses.

## SYSTEMATIC PALAEONTOLOGY

Specimens are housed in the Museum of Victoria, Melbourne (prefix NMVP), and Department of Geological Sciences, University of Canterbury, Christchurch (UCM). Most localities are entered on the Museum of Victoria locality register (NMVPL). Terminology, orientation and plate nomenclature follow Ubaghs (1967, 1969) and Ruta (in press), with modifications as in Ruta & Jell (1999a-c). All illustrations are of latex casts from decalcified moulds and whitened with ammonium chloride.

Class STYLOPHORA Gill & Caster, 1960
Order MITRATA Jaekel, 1918
Suborder ANOMALOCYSTITIDA Caster, 1952
Family ALLANICYTIDIIDAE Caster & Gill, 1967

DIAGNOSIS. See Ruta & Jell (1999a).

### **Notocarpos** Philip, 1981

TYPE SPECIES. *Notocarpos garratti* Philip, 1981 from the Ludlow Clonbinane Sandstone Member of the Humevale Formation, central Victoria; by original designation.

DIAGNOSIS (modified from Philip, 1981 and based on the largest available, undeformed specimens). Plate A about as wide as long, with long axis at about 45° to body axis, not in contact with left PLM. Plate B lacking. Plate C as wide as long, with subparallel lateral margins. LOP narrowly wedge-shaped. DLM with poorly developed truncatoconical projection, with process for spine insertion. C1 and C5 about 1.5 times as wide as long. C20 and C22 subrhomboidal, wider than long, with gently sinuous distal margins.

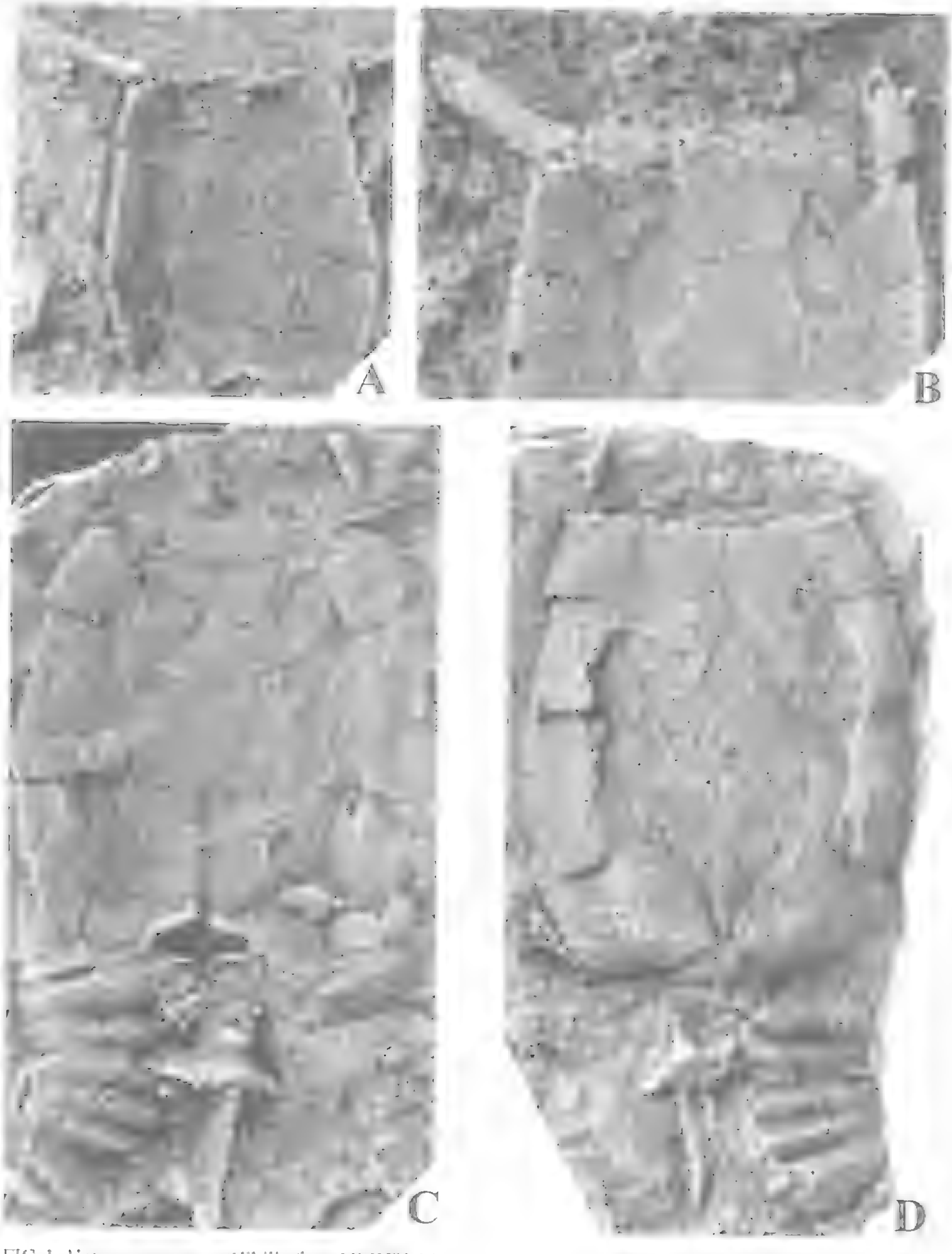



FIG. 1. *Notocarpos garratti* Philip from NMVPL300. A, plano-concave surface of NMVP100452, ×5. B, distal half of plano-concave surface of NMVP100453, ×8. C-D, plano-concave and convex surfaces, respectively, of NMVP100441, ×5

C21 twice as long as wide, occupying about 40% of width of convex surface, narrowly inserted between C20 and C22, with proximo-lateral margins smoothly concave, with proximal margin about 1/10 plate width, with straight lateral margins parallel to body axis. Spines straight, robust, cigar-shaped, without cutting lateral edges. Transverse ridge ornament on at least some part of A, C, DLM, ILM and PLM. C20 and C22 with same ornament laterally. Riblets and irregularly confluent, short transverse ridges laterally on C11, C13, C15 and C19. C21 without sculpture. Proximal part of appendage of 4 tetramerous rings overlapping each other to a small extent. Proximal styloid blade 1/3 width of distal blade, approximately semicircular, smooth. Distal blade massive, fan-shaped, with straight radiating ridges. Distal part of appendage narrow, truncated abruptly (probably incomplete in all available specimens), presumably not longer than body.

### **Notocarpos garratti** Philip, 1981
(Figs 1-11, 16A)

*Notocarpos garratti* Philip, 1981: 36, figs 3-6; Caster, 1983: fig. 2C.

MATERIAL. NMVP100459-100460, 22350-22351 from NMVPL299 (= F31 of Williams (1964)) in road cutting south of Bald Hills, c. 3.2km E of Kilmore, Victoria (Ludlow, Dargile Formation); NMVP100440-100445, 100449-100456, 21939-21942, 22349, 22353-22354 from NMVPL300 (= X64 of Williams (1964)) near disused mine on Comet Creek, c. 4.6km SE Clonbinane, Victoria (Ludlow, Clonbinane Sandstone Member, Humevale Formation); NMVP65008-65010, 65022-65028, 65030-65031, 65035-65038, 65040-65042, 65044, 65052-65053 from the type locality, in a cutting on Dry Creek Road, Clonbinane; mid Ludlow, Clonbinane Sandstone Member, Humevale Formation.

DIAGNOSIS. As for genus.

DESCRIPTION. EXTERNAL. (including only new or additional data not in Philip, 1981). MOP broadly trapezoidal, 1.5-2 times as wide as long, with straight distal margin. LOP wedge-shaped, with major axis at c.45° to body axis, narrowly inserted between MOP and DLM, with straight or convex lateral margins, with straight or concave medial margins. C21 much longer than wide, with concave proximo- lateral margins. C11 and C13 shorter than C15 and C19. C15 and C19 same size or larger than C20 and C22. Terrace-like ridges rarely extending across width of marginal plates of plano-concave surface, frequently replaced laterally by short ridges or riblets. Similar pattern on convex suface, except for more numerous riblets and confluent short ridges on lateral 2/3 of C11, C13, C15 and C19. External stereom texture usually compact to coarsely granular, rarely microporous or with vermicular surface pattern.

INTERNAL. C21 and C20 with system of ridges proximally (Figs 9A, 10C, 11). Ridges variable in width, meandering on C21 to form almost bilaterally symmetrical pattern, proximally consisting of straight left and irregularly sinuous right sections normal to proximo-lateral margins of plate running medially to points directly distal to left and right ends of proximal plate margin, distally in sinuous bilaterally symmetrical pattern with 2 lateral and 2 medial lobes. Distally the ridges recurve proximally in thin parallel left and right ridges; proximal ends separated by wide, medial, proximally tapering septum; septum slightly higher than ridges, with almost vertical lateral walls.

Ridge on C20 with first lobe after crossing from C21 V-shaped and apex pointing at co-operculum of C20; second lobe large, club-shaped, with medial arm crossing back to C21, curving latero-distally to surround right proximo-lateral angle of C21, continuing as thinner, straight ridge back on C20; third lobe subtrapezoidal, pointing towards co-operculum, with straight diverging arms; fourth and fifth lobes very weak ridges, finger-like; fifth lobe lateral to co-operculum. Co-operculum of C20 fan-shaped, raised, with slightly thickened margin, with proximal part continuing to proximo-lateral corner of plate as subtriangular, raised structure with almost straight medial margin and broadly concave lateral margin, distally with thick subquadrate body on margin centro-distally; faint, distally concave ridge projecting laterally from co-operculum, almost parallel to proximal arm of fifth lobe, widening and fading laterally.

Orifice platelets overlying transverse thickening on distal interior of C1 and C5, 6-8 in transverse row, rectangular, 1mm wide, 0.75mm long (Figs 5C, 8A).

APPENDAGE. Proximal part of appendage about 1/5 body length, <1/3 body width. Tetramerous rings 4, overlapping each other narrowly, with thickening along distal margins, gently arcuate transversely. Proximal styloid blade smooth, as long as wide, 1/3 distal blade width, slightly broader than and hardly separated from central part of styloid, with roughly semi-circular thick free margin, with convex distal

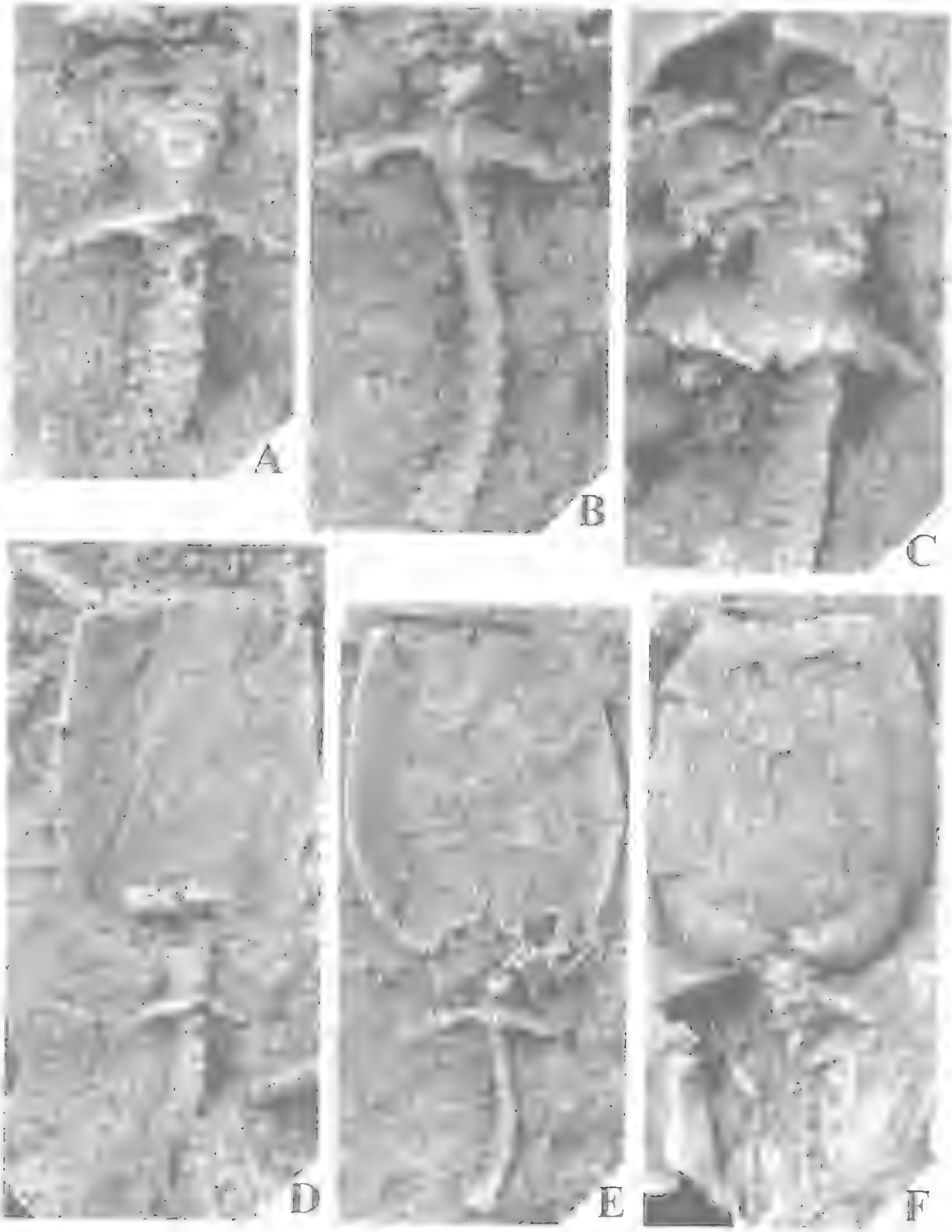



FIG. 2. *Notocarpos garratti* Philip from NMVPL300. A,D, detail of proximal appendage and plano-concave surface respectively of NMVP100453, ×10 and ×5, respectively. B,E, detail of proximal appendage and plano-concave surface of NMVP100443, ×8 and ×5, respectively. C, detail of proximal appendage of NMVP100441, ×10. F, convex surface of NMVP100440, ×5.

surface, sometimes exceptionally well-developed and flared (Fig. 10B,D). Distal styloid blade transversely expanded, fan-shaped, slightly recumbent proximally, with sharp free margin, with weak straight radial ridges on proximal and distal surfaces (Fig. 9A,C-D); ridges of proximal surface slightly more robust and wider medially than laterally; ridges of distal surface slightly wider and flatter than on proximal surface; lateral ear-like projections with flat to gently depressed proximal surfaces and semicircular to parabolic margins. Appendage incomplete in most specimens. Ossicles and plates similar to those of *Placocystella africana* in lateral view (Ruta & Theron, 1997); ossicles with slightly more sinuous proximal and distal margins, with apical margin at 45° to horizontal plane, with apex projecting distally, with knobbly sculpture on lateral surfaces. External stereom texture of appendage similar to that of body, sometimes irregular due to coarse, irregular ridges, pustules and shallow pits, especially on tetramerous rings and styloid.

MORPHOGENY. In smallest specimens: length/width ratio of body slightly greater; lateral body margins more convex in proximal 1/3; plate A at least twice as long as wide; MOP as long as wide; proximal and distal margins of DLM and ILM more strongly converging medially; DLM wider than long; angle between lateral and medial margins of C1 and C5 >120°; lateral and medial margins of C1 and C5 sometimes merging into each other along smooth curve; lateral and distal margins of C20 and C22 merging gradually into one another along gently convex curve in plan view, without forming latero-distal angle; C11 and C13 as long as or longer than C15 and C19; C15 and C19 smaller than C20 and C22; proximolateral margins of C21 gently sinuous, diverging at greater angle from longitudinal axis; C21 width/body width slightly higher; C21 length/C1 (C5) length ratio slightly lower; spines more robust, shorter than distal body margin, club-shaped; proximal part of appendage <1/5 as long as body, at least 1/2 as wide distally as proximally; distal styloid blade >1/2 body width; ridges on both surfaces of the body frequently interrupted and replaced by riblets or transversely aligned short ridges; most distal ridges often pustule-like, especially on convex surface.

REMARKS. Although preservation is sometimes poor due to relatively coarse matrix and despite little deformation in some specimens, new material of *Notocarpos* supplements information on external ornament of body plates and styloid. Previously unrecorded features include the rectangular orifice platelets on the inside of C1 and C5 and the system of sinuous ridges on interior proximal 1/2 of convex surface. The latter feature has been documented only in *Allanicytidium* and *Placocystella* among allanicytidiids (Caster & Gill, 1967; Ruta & Theron, 1997). Orifice platelets are known in some Northern Hemisphere anomalocystitids (Jefferies & Lewis, 1978; Kolata & Guensburg, 1979; Kolata & Jollie, 1982; Parsley, 1991).

### **Tasmanicytidium** Caster, 1983

TYPE SPECIES. *Tasmanicytidium burretti* Caster, 1983 from the Lower Silurian Richea Siltstone, Tasmania; by original designation.

DIAGNOSIS. (modified from Caster, 1983). Plate A as long as and c. 1/3 as wide as C; A-C suture straight. LOP-DLM suture strongly concave distally. DLM with latero-distal angles subcylindrical for spine insertion. C20 and C22 with weak transverse keels occupying more than 1/2 of plate width. C21 shield-like, with most proximal part narrowly inserted between C20 and C22, with gently concave proximal margin very narrow. Spines round in cross-section, straight, needle- shaped. Scale-like riblets on lateral 1/2 of PLM and on C11, C13, C15, C19, C20, and C22. C20 and C22 with few, short, transverse terrace-like ridges proximo-laterally.

### **Tasmanicytidium burretti** Caster, 1983 (Figs 12, 16B)

*Tasmanicytidium burretti* Caster, 1983: 334, figs 2-4.

MATERIAL. NMVP148541 from NMVPL296 near Terry Walshe Road, Tiger Range, on 1:100,000 Wedge Sheet 8112 DN512850, Tasmania; Llandovery, Richea Siltstone (Baillie, 1979).

DIAGNOSIS. As for genus.

DESCRIPTION. EXTERNAL. Largest riblets on convex surface scale-like, closely spaced, with straight to irregular distal margin, confined to C20-C22, about 0.2mm wide; smallest riblets subcircular, sparse, conferring pustulose aspect to distal part of convex surface, about 0.1mm wide (Fig. 12B). Transverse ridges on C20 and C22 faint. Riblets on C15 and C19 never confluent, irregularly spaced, scale-like or sub-rectangular proximally, subcircular to pustulose distally. Riblets on C11 and C13 sparse, small,

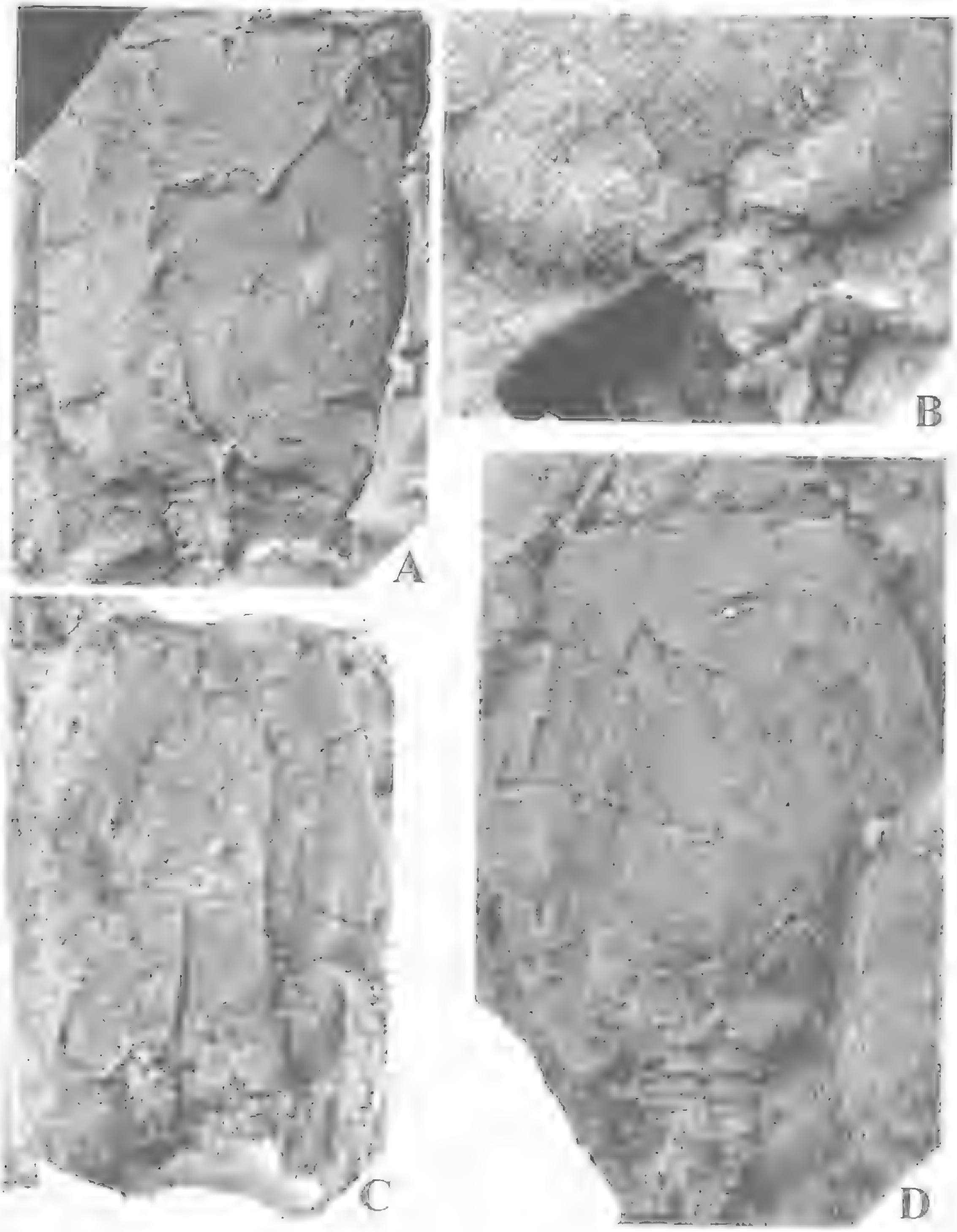



FIG. 3. *Notocarpos garratti* Philip from NMVPL300. A,C. convex and plano-concave surfaces of NMVP100445, ×3. B. proximal convex surface and appendage of NMVP100440, ×10. D. convex surface of NMVP100442, ×4.

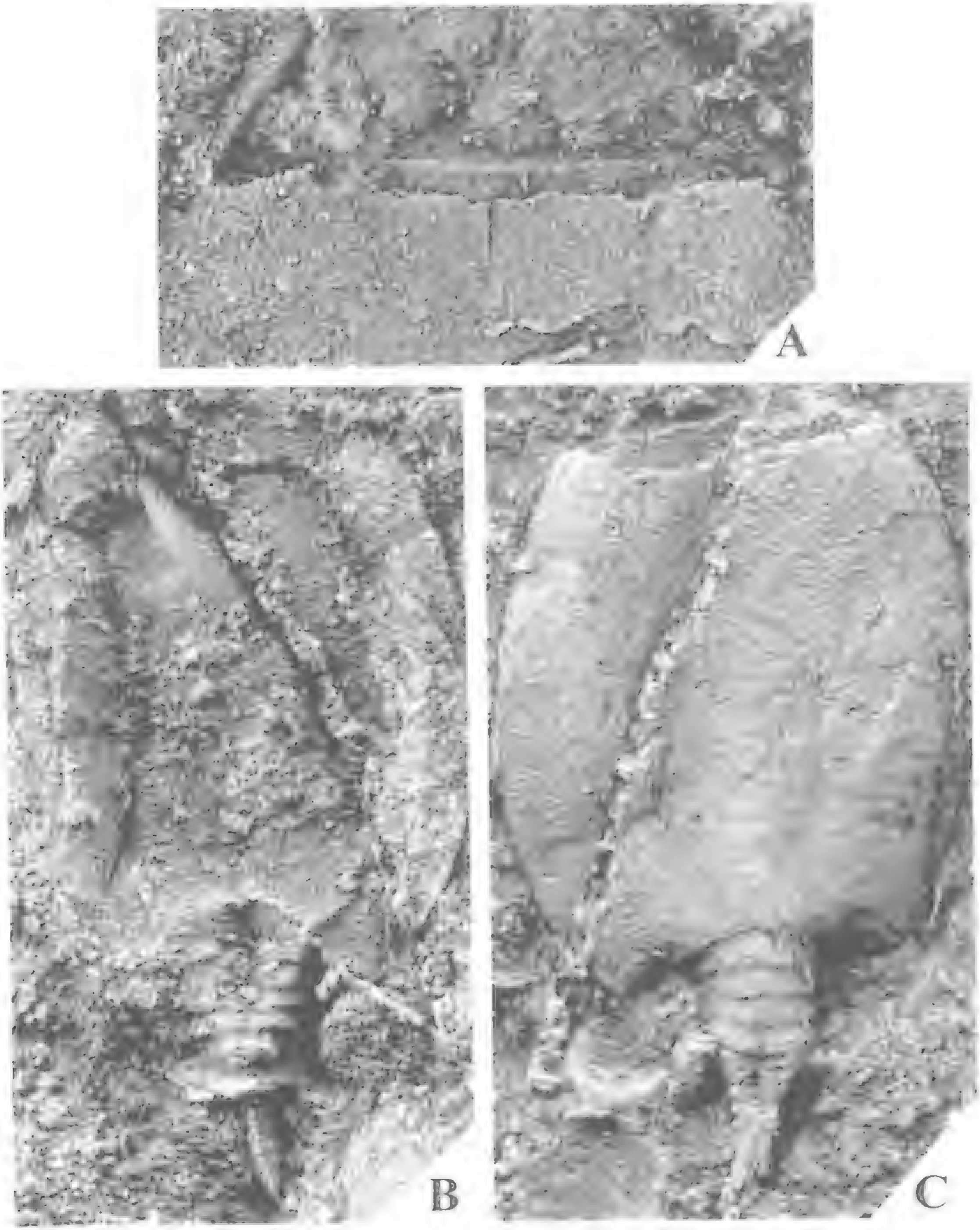



FIG. 4. *Notocarpos garratti* Philip from NMVPL300. A, detail of distal part of convex surface of NMVP100442, ×8. B-C, plano-concave and convex surfaces, respectively of NMVP21939, ×5.

pustulose. Riblets on C21 varying in shape and size proximo-distally, uniformly distributed C21 with narrow, marginal zone of short, transverse striations. Stereom fabric apparently

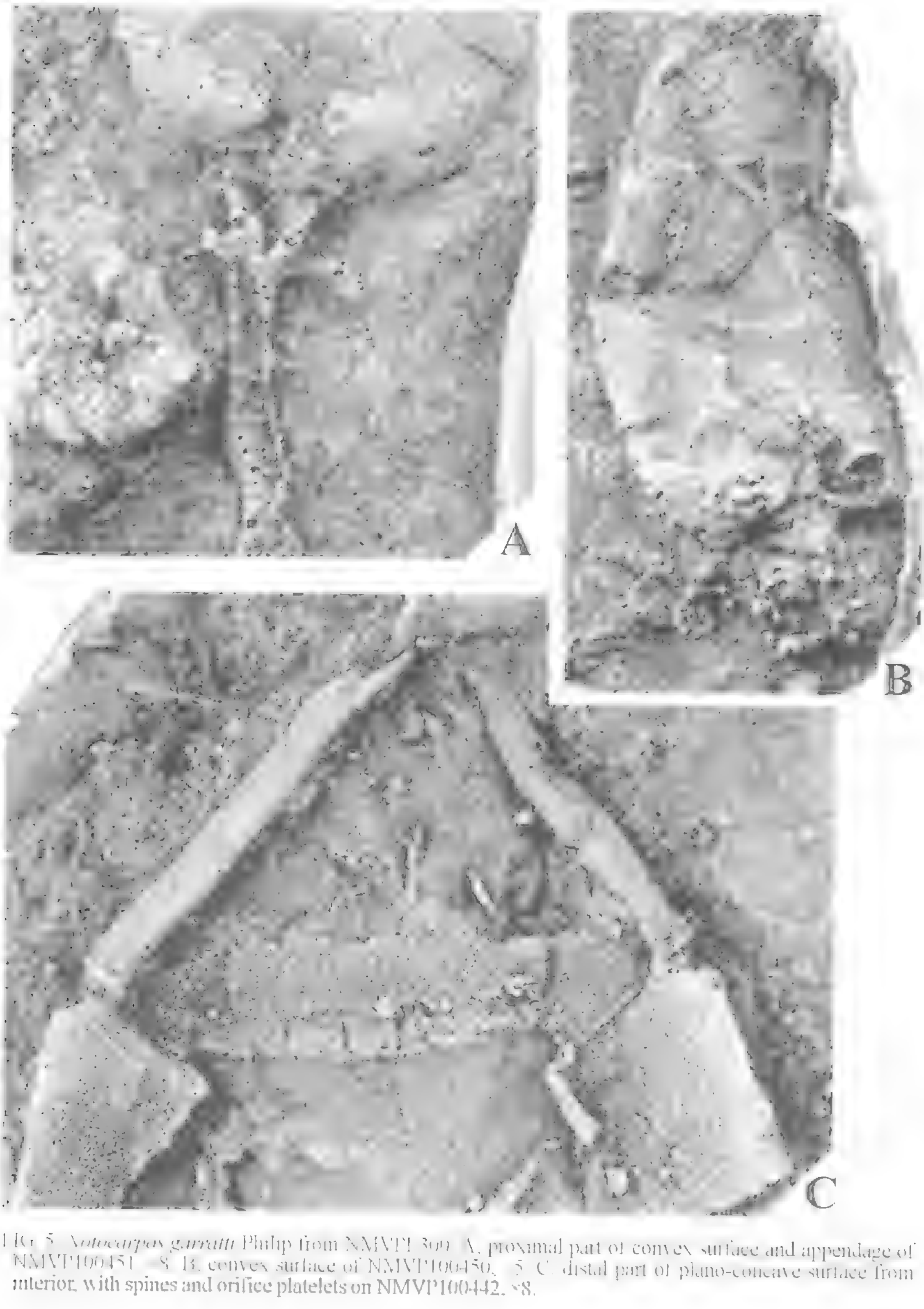



FIG. 5. *Notocarpos garratti* Philip from NMVPL300. A, proximal part of convex surface and appendage of NMVP100451, ×8. B, convex surface of NMVP100450, ×5. C, distal part of plano-concave surface from interior, with spines and orifice platelets on NMVP100442, ×8.

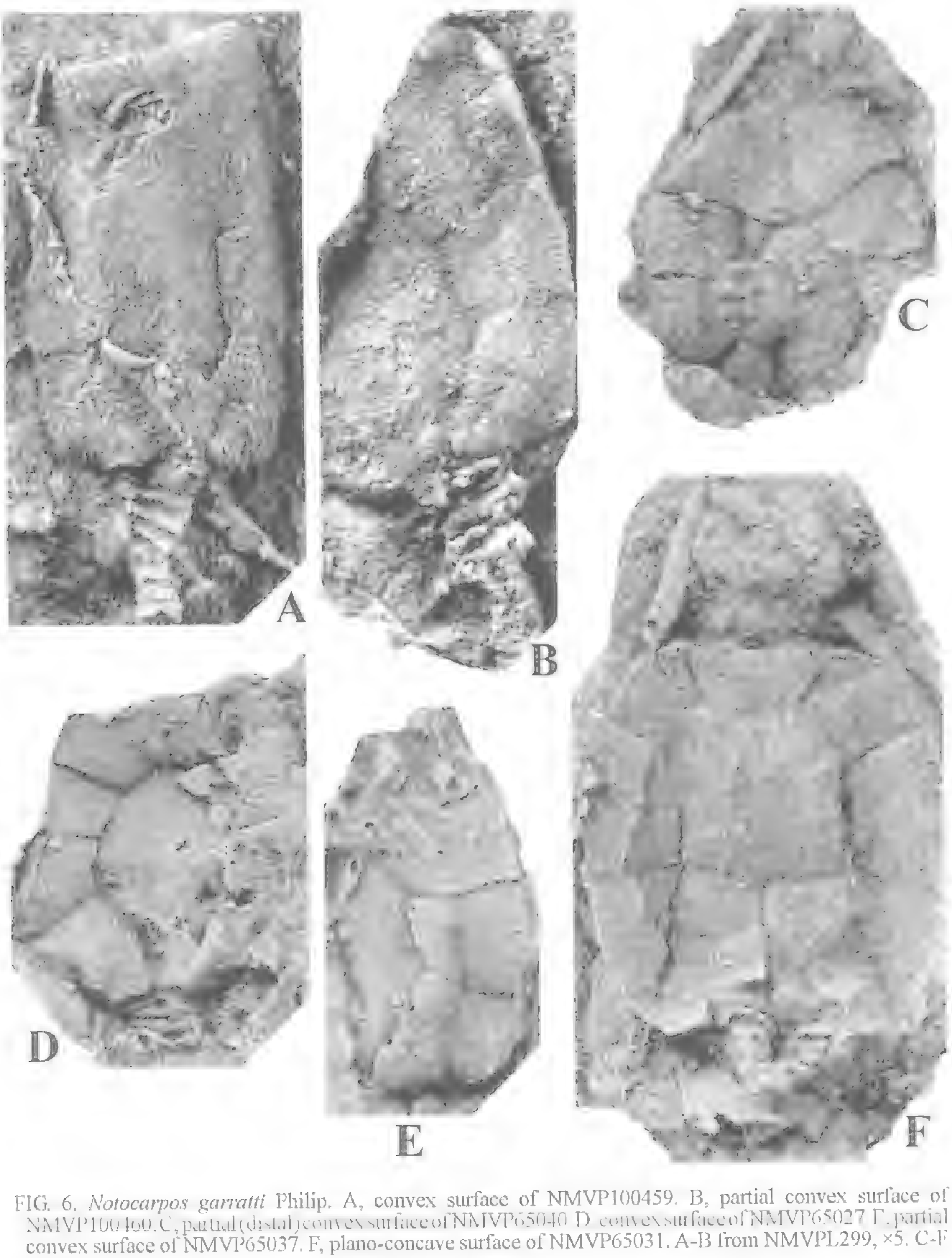
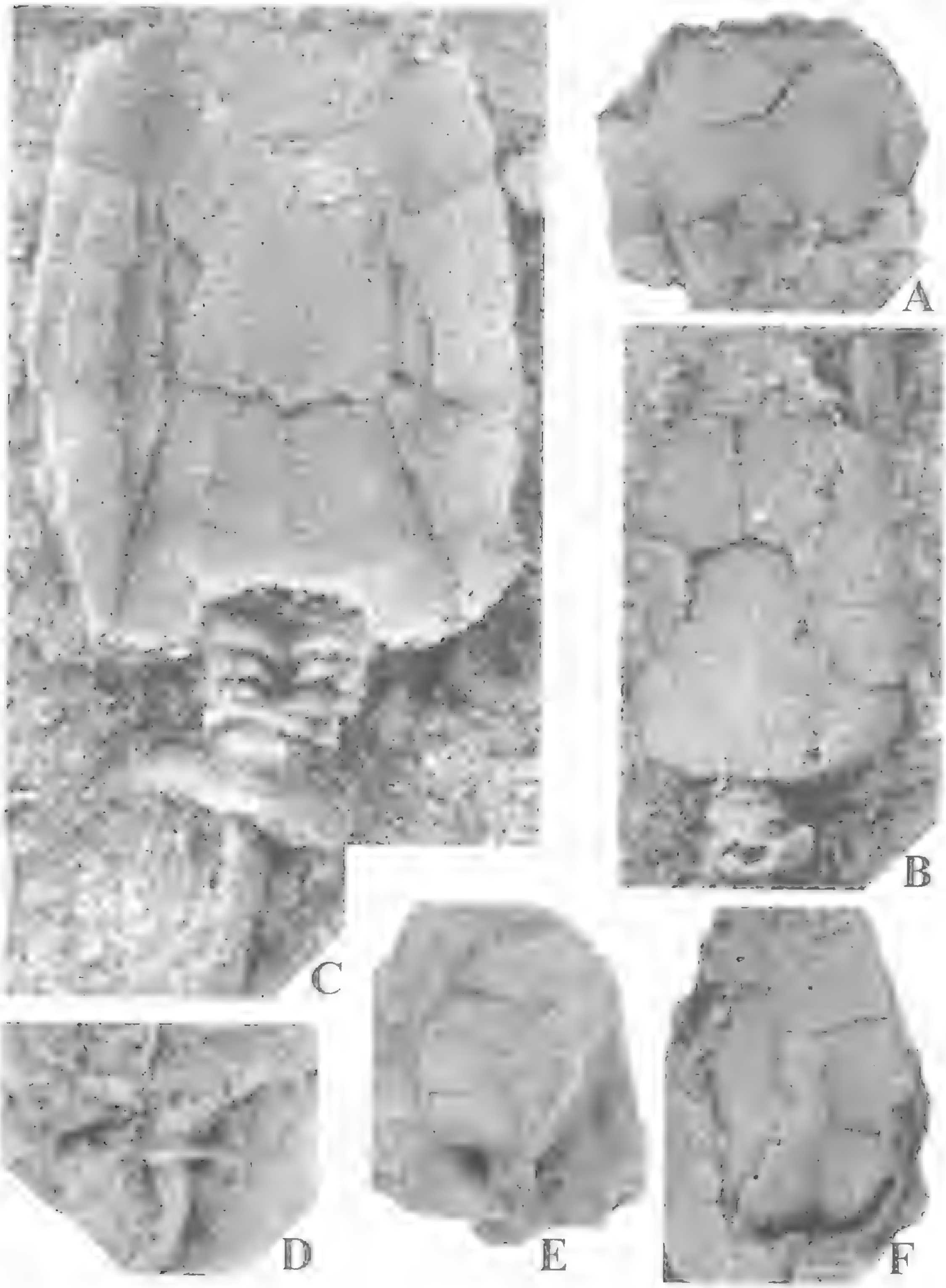



FIG. 6. *Notocarpos garratti* Philip. A, convex surface of NMVP100459. B, partial convex surface of NMVP100460. C, partial (distal) convex surface of NMVP65040. D, convex surface of NMVP65027. E, partial convex surface of NMVP65037. F, plano-concave surface of NMVP65031. A-B from NMVPL299, ×5. C-F from G23, ×3.


A
B
C
D
E
F

microporous to compact. Stereom centrally on C1 and C5 of irregular, subcircular shallow pits separated by weak trabeculae, proximally compact or minutely porous, distally vermicular, with irregularly sinuous, thick bifurcating trabeculae separated by shallow, narrow furrows and often flanked by short thickenings of variable shape and size.

INTERNAL. C5 and C13 with laterally displaced, subhemispherical thickenings. C21 with subcentral straight ridge on proximal half surrounded by poorly defined, sinuous ridges as in *Allanicytidium* and *Notocarpos*. Distal margin of C1 and C5 with transverse row of 5-6 central subquadrate orifice plates, 0.3-0.5mm wide, bordered proximally by smaller, rectangular platelets. Orifice plates and inside of convex surface with compact to microporous stereom.

APPENDAGE. Tetramerous ring plates of convex side arcuate in cross-section, with thin ridge running close to the thickened distal margins. Styloid with large distal blade; blade with concentric, externally convex, closely spaced ridges on proximal (Fig. 12A) and distal surfaces (Fig. 12B), arranged in sectors delimited by radial furrows running on distal surface from insertion of blade on styloid to blade margin, and corresponding to radial ridges with zig-zag course on proximal surface; concentric ridges alternating on both sides of zig-zag ridges and radial furrows, with degree of curvature increasing in more apical sectors (i.e. sectors which are closer to midpoint of blade margin).

REMARKS. The new specimen adds information on orifice plates, tetramerous rings of appendage, shape and ornament of styloid blade, external body sculpture and inside of convex surface. The specimen is slightly deformed, but the convex surface is fully articulated. Comparison with the holotype permits an approximate estimate of body outline and general proportions. The elongate-ovoid or vasiform body (Caster, 1983) is almost certainly a genuine feature, although it may be slightly exaggerated in Caster's reconstruction.

## **Allanicytidium** Caster & Gill, 1967

TYPE SPECIES. *Allanicytidium flemingi* Caster & Gill, 1967 from the Lower Devonian Reefton Group, New Zealand; by original designation.

DIAGNOSIS. (modified from Caster & Gill, 1967). Body subquadrate to ovoid, with broad margined re-entrant for insertion of appendage. A and C longer than wide, almost mirror images of each other. DLM with latero-distal angles projected into subconical processes for spine insertion. C1 and C5 thickened internally along distal margin, with sinuous proximo-lateral margins. C11 and C13 approximately equal in size to C1 and C5, with broadly concave medial margins and irregular proximal margins. C15 and C19 2/3 size of C11 and C13, each with sinuous proximal margin. C20 and C22 larger than C15 and C19, as wide as long. C21 with concave proximo-lateral margins interrupted by marked expansion in proximal half, with straight subparallel lateral margins. Closely spaced, polygonal to scale-like riblets on lateral marginal plates of plano-concave surface, near lateral margins of A and C and along most of the lateral margins of PLM. Proximal styloid blade semicircular, with thick, radial ridges on its distal surface. Distal styloid blade much wider than tall. Ossicles with lateral vertical grooves and poorly developed, nodose apices.

### **Allanicytidium flemingi** Caster & Gill, 1967 (Figs 13-15, 16C)

*Allanicytidium flemingi* Caster & Gill, 1967: S564, figs 360, 361; Caster, 1983: figs 1, 2A.

MATERIAL. NMVP27474 (plaster replica of holotype NZGS38/370203) and UCM440 from Rainy Creek near Reefton, Westland, South Island, New Zealand in the Emsian, Reefton Group.

DIAGNOSIS. As for genus.

DESCRIPTION. EXTERNAL (Figs 13, 14A). Riblet size (0.1-0.5mm wide), shape and distribution variable on different plates and on the same plate of convex surface. Riblets closer together on lateral 1/2 of marginal plates. Largest riblets on lateral 1/2 of C15, C19, C20 and C22, crescent-shaped, rectangular or irregularly polygonal, in irregular transverse rows, often resulting in vermicular surface, as opposed to

FIG. 7. *Notocarpos garratti* Philip. A, convex surface of NMVP65028. B, convex surface of NMVP22354. C, plano-concave surface of NMVP21941. D, proximal appendage of NMVP65053. E, convex surface of NMVP65035. F, convex surface of NMVP65037. A, D-F from G23, all ×3. B-C, from NMVPL300, ×8 and ×6, respectively.

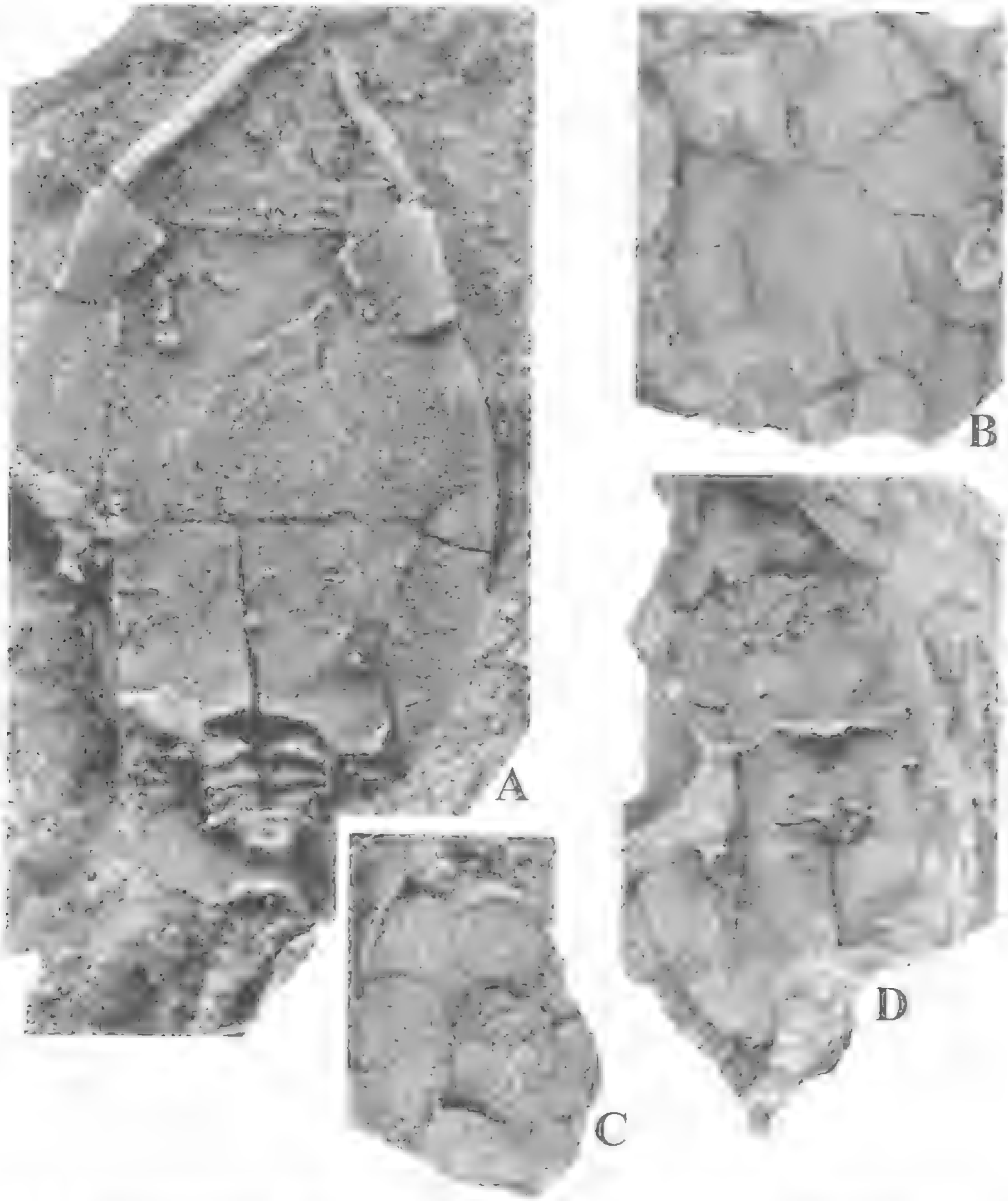



FIG. 8. *Notocarpos garratti* Philip. A, exterior view of plano-concave surface of NMVP100442 from NMVPL300, ×4. B, convex surface of NMVP65042. C, partial convex surface of NMVP65025. D, partial plano-concave surface of NMVP65044. B-D, from G23, ×3.

tuberculate or scaly elsewhere. Smallest riblets distally and proximo-medially on C20 and C22 and on proximal 1/2 of C21, generally scale-like to broadly rounded, slightly wider than long, with poorly defined margins, sometimes reduced to small pustules without distal slope. Riblets on C21 less pronounced than those on lateral 1/2 of marginal plates, with more regular, convex distal

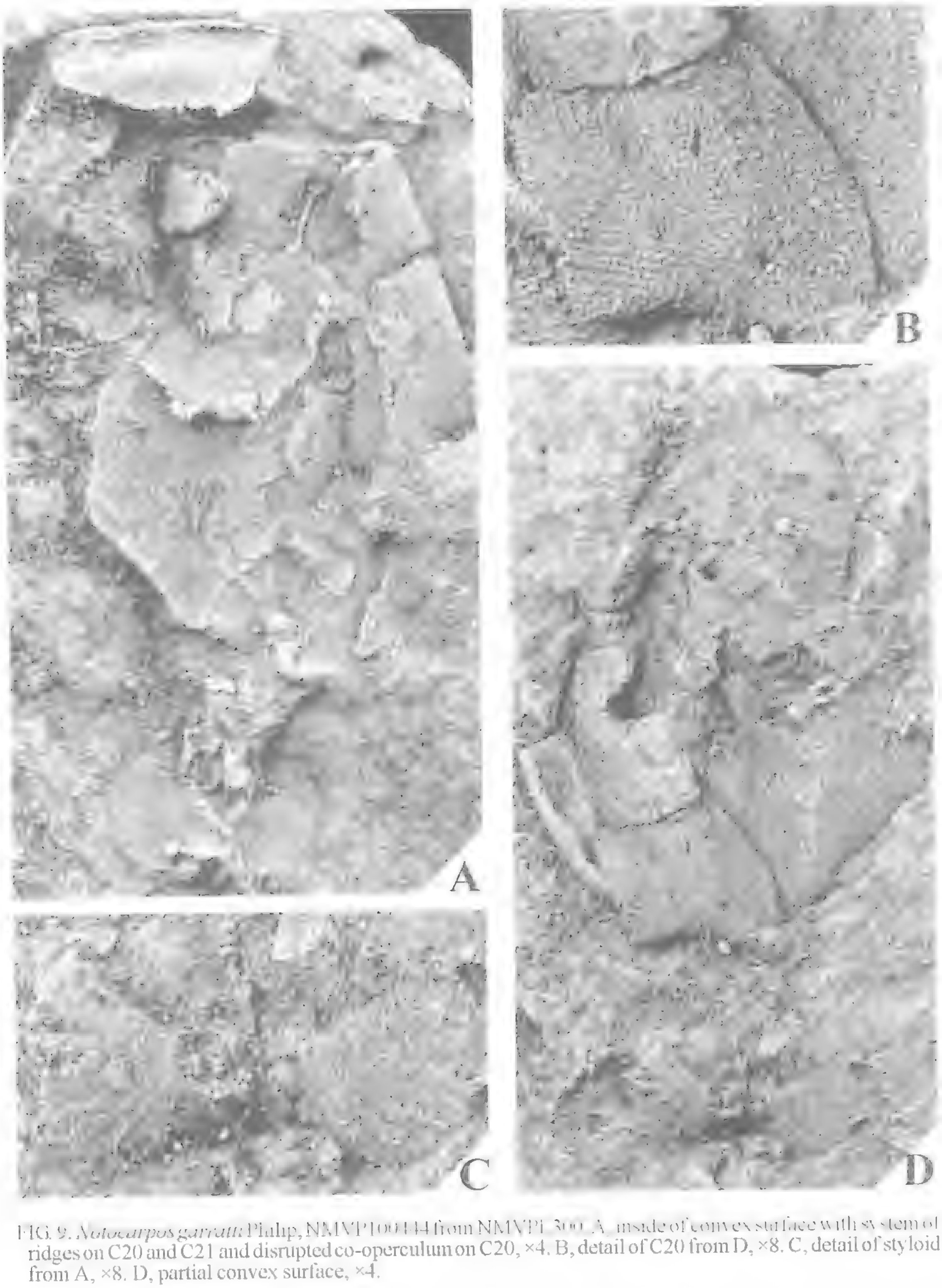


FIG. 9. *Notocarpos garratti* Philip, NMVP100444 from NMVPL300. A, inside of convex surface with system of ridges on C20 and C21 and disrupted co-operculum on C20, ×4. B, detail of C20 from D, ×8. C, detail of styloid from A, ×8. D, partial convex surface, ×4.

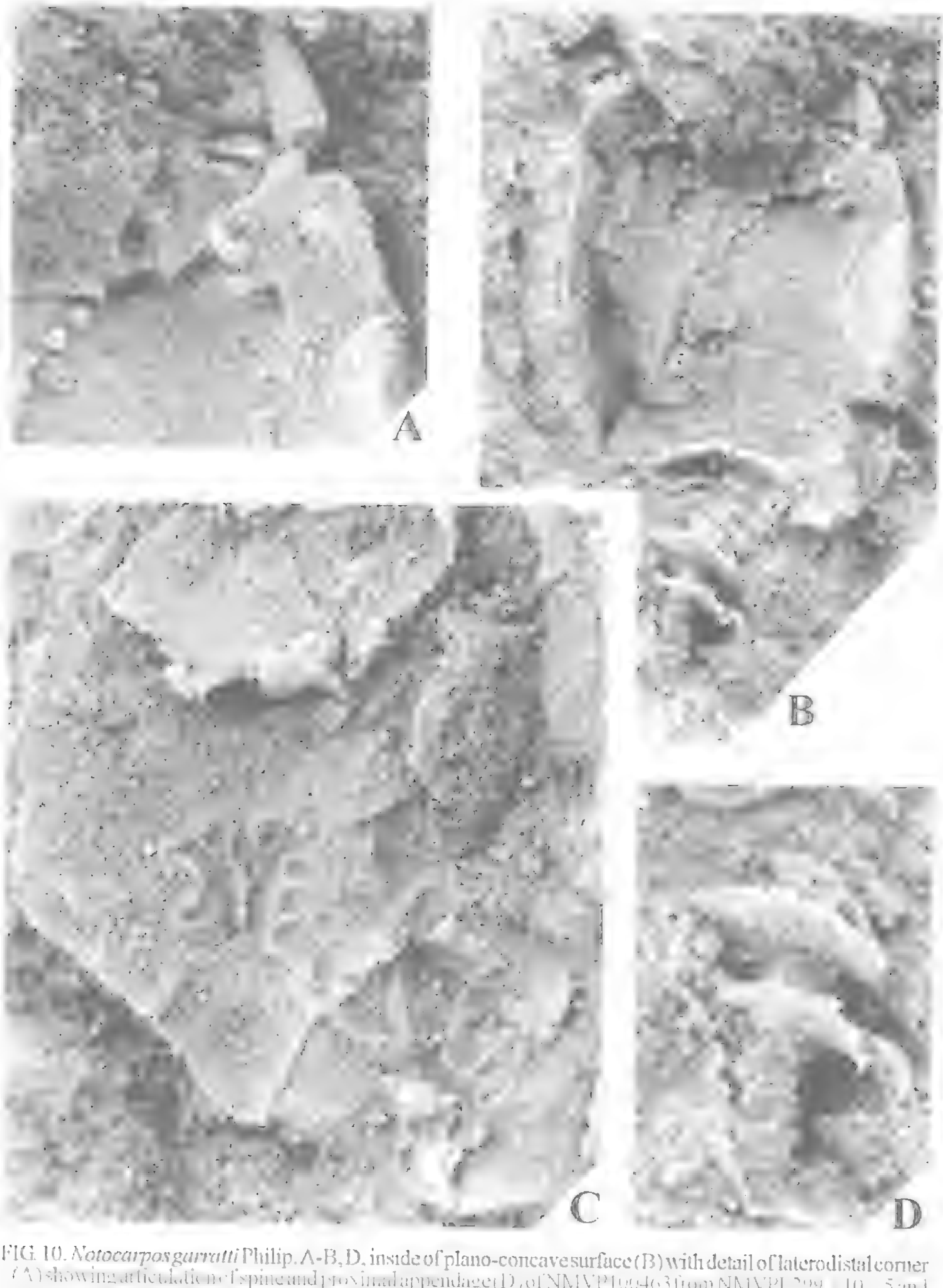



FIG. 10. *Notocarpos garratti* Philip. A-B, D, inside of plano-concave surface (B) with detail of laterodistal corner (A) showing articulation of spine and proximal appendage (D), of NMVP100463 from NMVPL299, ×10, ×5 and 10, respectively. C, inside of C20 and C21 of NMVP100444 from NMVPL300, ×8

margins, 1.5 times wider than long. Riblets on marginal plates 1.5-3 times as wide as long, with sharp, straight to crescentic, rarely polygonal distal margins.

INTERNAL (Figs 14B-C, 15A). Internal surface of lateral marginal plates finely granular, of small irregular pores and furrows. Deeper portions of stereom sponge-like to coarsely perforate, especially on C21. Peripheral bands, corresponding to external bands, of fibrillar stereom composed of parallel striations perpendicular to plate margins and intercalated with transversely elongate to subcircular pores. Bands divided into lateral part and medial part by thin ridge reaching maximum thickness along distal margins of marginal plates and latero-distal margins of C21; medial part 2-3 times as wide as lateral part. Portion of band running along distal angle of C21 1.5 times wider than elsewhere, with coarse stereom, without radial pattern of trabeculae in proximal 1/2, with fine, closely spaced, short trabeculae forming a fringe in distal 1/2 (Fig. 14B-C). Subelliptical, proximo-distally elongate, subcentral thickenings on lateral marginal plates of convex surface, with slightly raised margins. Thickening stereom compact peripherally, porose to sponge-like centrally.

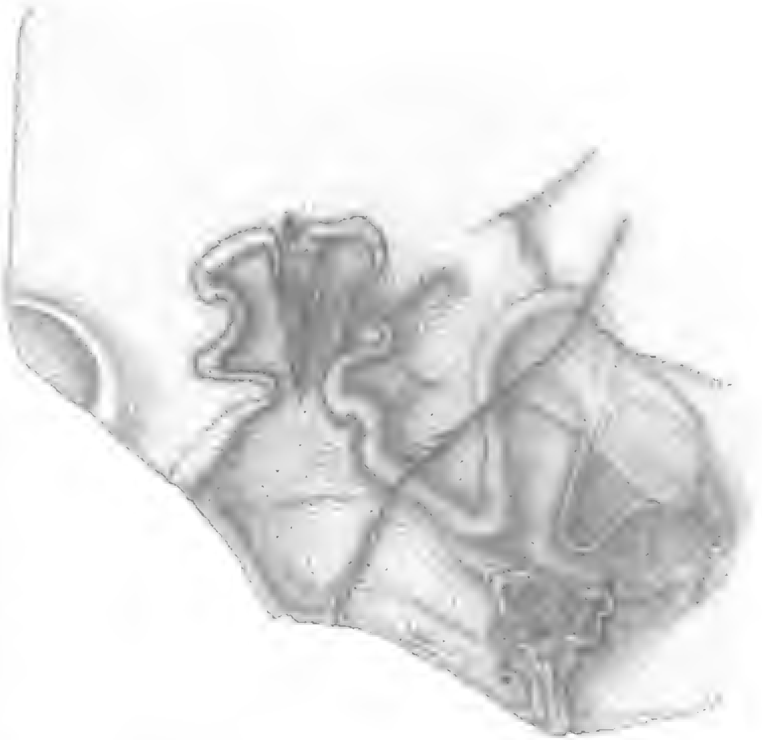


FIG. 11. Camera lucida drawing of system of ridges on internal surface of C20 and C21 in *Notocarpos garratti* Philip, based on NMVP100444.

*Stereom* (Figs 13-14). External skeleton of microporous stereom without surface pattern. Surface of largest riblets coarsely granular to compact, with minute pores in smallest ones. Stereom near plate margins of larger pores of more irregular shape than those on central part of plates. Plate margins bordered by band 0.2-1mm wide, generally without riblets and with stereom of fine, closely spaced, straight parallel trabeculae and subcircular irregularly distributed pores. Changes of stereom structure through plate thickness visible if skeletal surface is eroded or broken. Stereom of deeper parts of skeleton generally coarser than surface stereom, labyrinthine, of short irregular thin branching trabeculae delimiting irregular pores. Deeper stereom at level of peripheral bands composed of sinuous, branching trabeculae delimited by irregular furrows, replaced by granular fabric immediately adjacent to margins.

*Proximal body excavation.* Proximal margins of PM crescent-shaped, with medial 1/2 slightly raised above subhorizontal projections (Fig. 15A). Apophyses subvertical, c. 1/2 as wide as each PM, subtriangular, with 1/3 of external surface closer to proximal margins of PM almost flat, remainder gently convex, with lateral ends turning abruptly towards convex surface and continuing into bases of apophyseal horns. Left horn missing. Right horn of uniform width, slightly distal to apophysis, subhorizontal, flat in cross-section, with free margins gently convex externally and only slightly diverging latero-medially (Fig. 15B). Medial end of right horn truncated abruptly without signs of breakage, therefore presumably complete, straight, oblique to longitudinal axis, reaching point at c. 2/3 of apophysis width in latero-medial direction. Space between internal margin of right horn and apophysis transversely

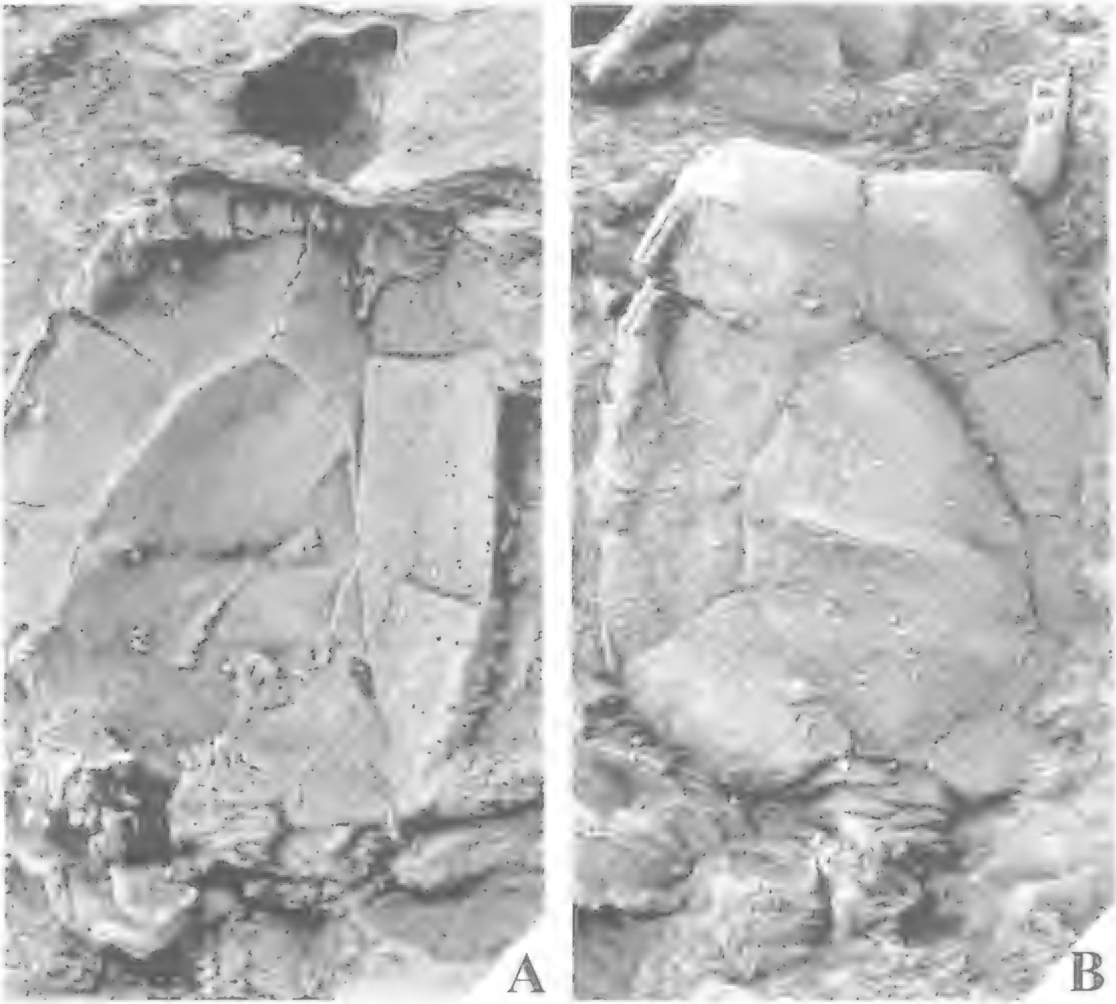



FIG. 12. *Tasmanicytidium burretti* Caster, incomplete plano-concave surface, external (B) and partially disrupted internal side(A) of convex surface, broken left spine, body sculpture, tetramerous rings and styloid with external ornament on distal blade. NMVP148541 from NMVPL296, ×6.

elongate, tapering slightly latero-medially and bent gently towards plano-concave surface.

REMARKS. Caster & Gill (1967) gave a succinct but comprehensive description of *Allanicytidium* based on an almost complete external mould of the plano-concave surface and internal mould of the convex surface of a single individual (see also Caster, 1983). Replicas of type material in the Museum of Victoria include the partial external mould of the convex surface of the holotype, illustrated here for the first time together with a second specimen. Both individuals provide data on external sculpture and changes in stereom fabric of the interior of the convex surface, the shape of C21 (especially its proximal 1/4) and the morphology of the proximal body excavation. Knowledge of other skeletal features (e.g. MOP; internal side of plano-concave surface; ornament of distal styloid blade and distal ossicles) is still not available.

## SUMMARY AND CONCLUSIONS

Configuration of the convex surface of the 3 allanicytidiids discussed herein (Fig. 16A-C) are compared to that of *Placocystella africana* (Fig. 16D). Although similar to *Allanicytidium flemingi*, the Lower Devonian *Australocystis langei* Caster, 1956 from Brazil is omitted from the following discussion because of the incomplete preservation of its convex surface

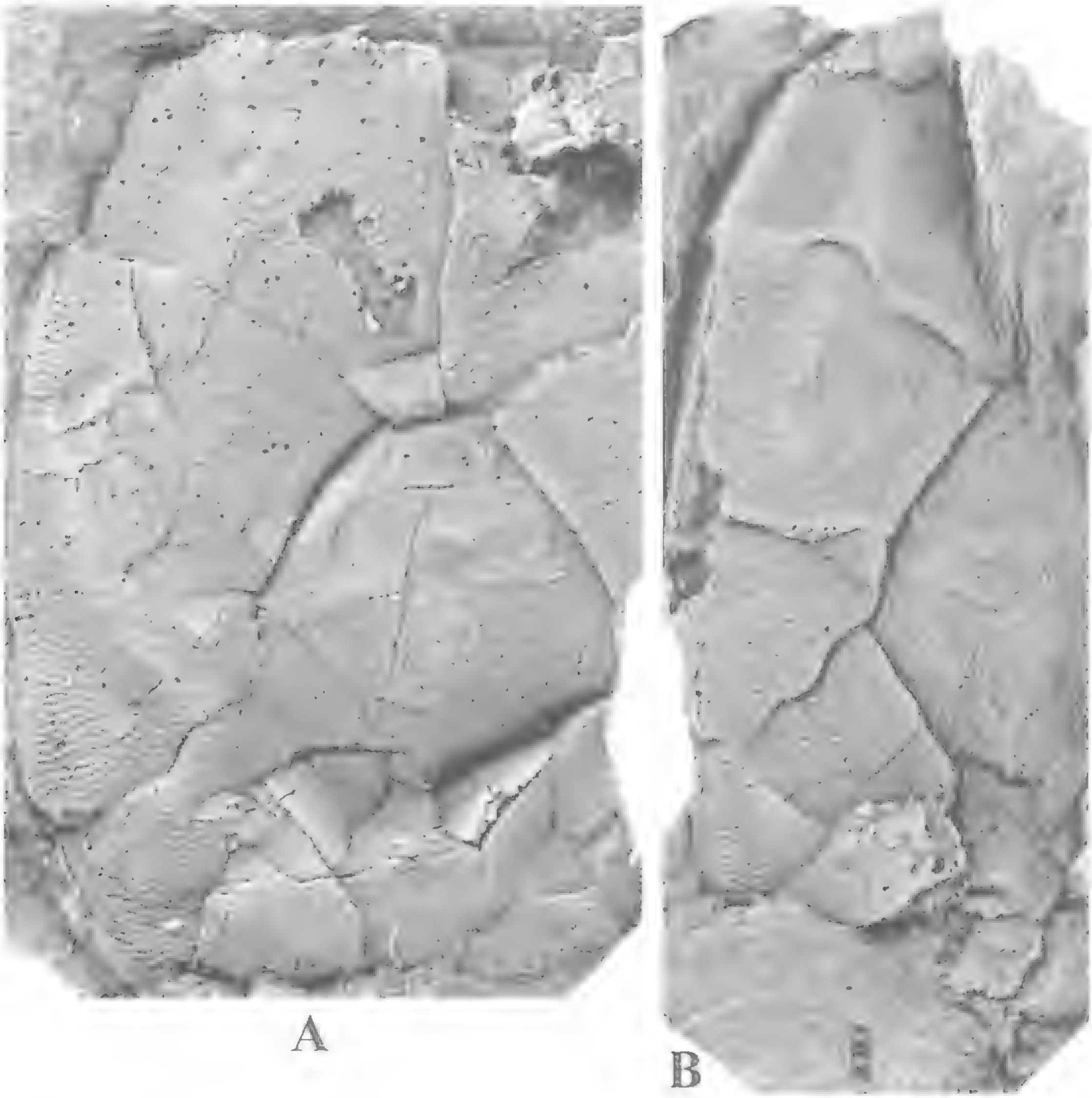



FIG. 13. *Allanicytidium flemingi* Caster & Gill, from Rainy Creek near Reefton, NZ. A, partial convex surface and body sculpture of UCM440, ×5. B, partial convex surface of NMVP27474 (replica of holotype NZGS 38/370203), ×5.

(Ruta & Theron, 1997; Ruta, in press). The proximal neck-like region in C21 in *Allani- cytidium* and *Placocystella* suggests that these taxa are closer to each other than either is to *Tasmanicytidium* or *Notocarpos* (Ruta & Theron, 1997; Ruta, in press). In *Tasmanicytidium*, the neck is not developed, but a short subtrapezoidal region between the proximo-medial angles of C20 and C22 indicates where the neck developed in more derived allanicytidiids. In passing from *Tasmanicytidium* through *Placocystella* to *Allanicytidium*, the C20/C21 and C21/C22 sutures became progressively more tortuous, resulting in development of lateral angular projections, poorly developed and close to the proximal margin of C21 in *Placocystella*, prominent and displaced halfway along the length of the neck in *Allanicytidium*.

External sculpture in *Notocarpos* has transitional features between those of certain anomalocystitids from the Northern Hemisphere (e.g. *Placocystites forbesianus* de Koninck,

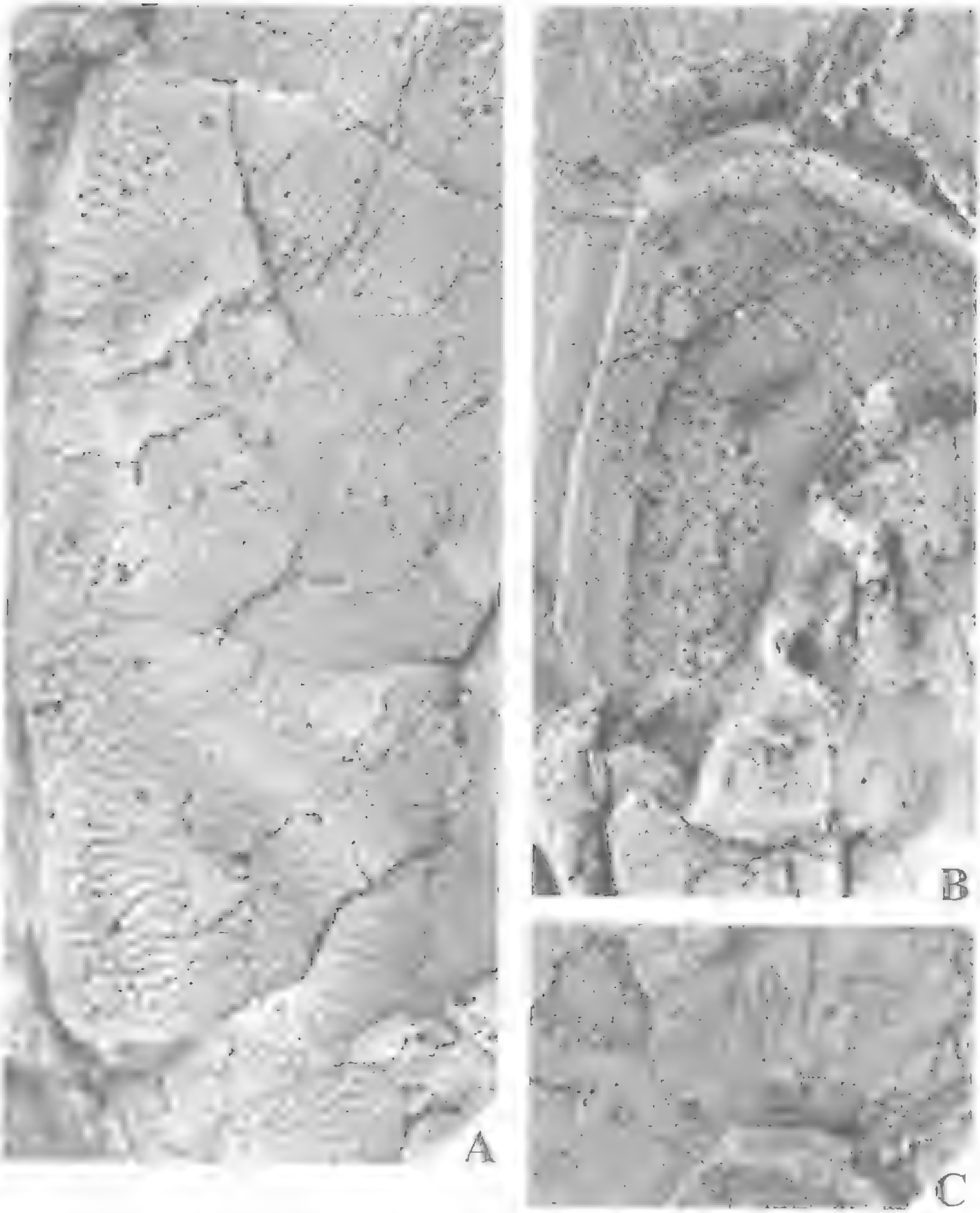



FIG. 14. *Allanicytidium flemingi* Caster & Gill, UCM440, from Rainy Creek near Reefton, NZ. A, detail of sculpture and stereom fabric of convex surface, ×10. B,C, inside of distal part of C21, showing peripheral band, ×10 and ×8, respectively.

1869; Jefferies & Lewis, 1978) and those of more derived allanicytidiids. In the light of Jefferies' (1984) reconstruction of ontogenetic changes in *Placocystites*, Ruta & Theron (1997) and Ruta (in press) invoked paedomorphosis to explain the sculpture pattern of the allanicytidiids

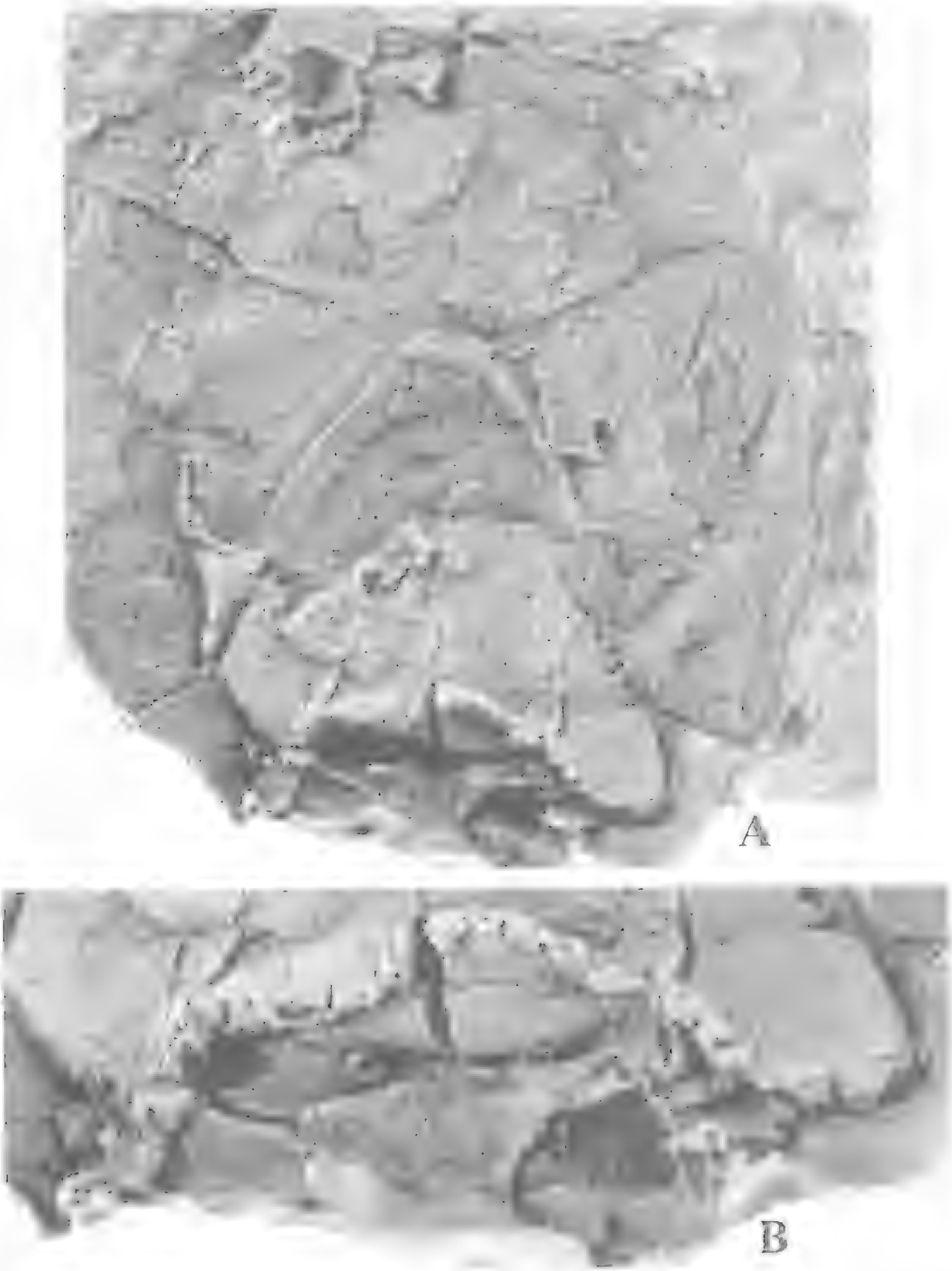


FIG. 15. *Allanicytidium flemingi* Caster & Gill, UCM440, from Rainy Creek near Reefton, NZ. A, inside of convex surface showing stereom fabric and peripheral bands, ×5. B, proximal body excavation with apophyseal horns, ×10.

Paedomorphic changes in allanicytidiid evolution are suggested by the smallest specimens of *Notocarpos* with sculpture of short ridges or riblets. The strongly diverging proximo-lateral margins of C21 in young *Notocarpos* are reminiscent of those of more derived allanicytidiids (e.g. *Tasmanicytidium* and *Placocystella*). It is possible that paedomorphic changes occurred repeatedly in the allanicytidiid clade and affected various structures (ornament; plates) differently.

Few changes affected the general plating pattern of the body (Ruta & Jell, 1999a). These involve relative proportions of MOP, LOP, A and C plates, on the plano-concave surface, and outline of C21, on the convex surface. A detailed analysis of character changes is provided by Ruta (in press).

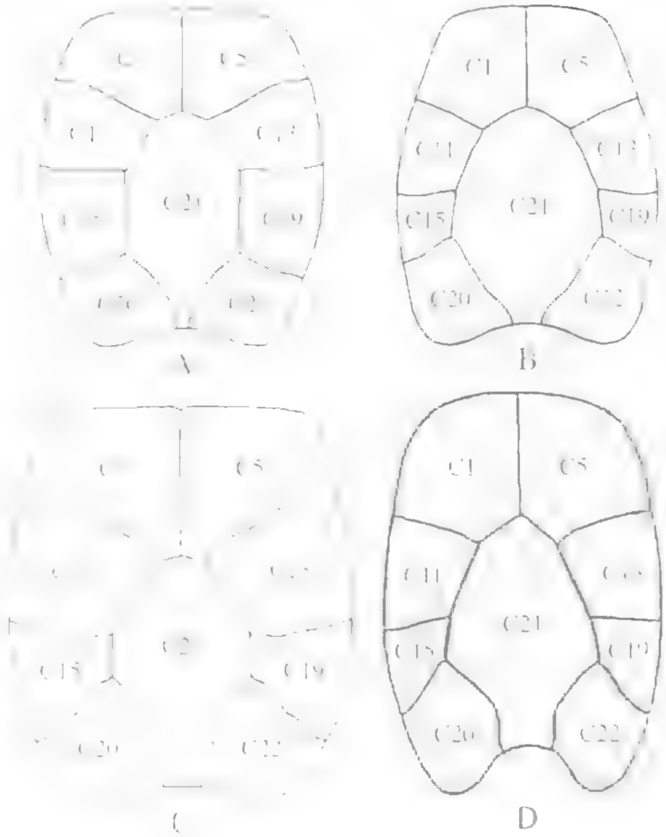



FIG. 16. Reconstruction of plating pattern of convex surface in *Notocarpos garratti* Philip (A), *Tasmanicytidium burretti* Caster (B), *Allanicytidium flemingi* Caster & Gill (C) and *Placocystella africana* (Reed) (D). Drawings not to scale.

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## LITERATURE CITED

BAILLIE, P.W. 1979. Stratigraphic relationships of Late Ordovician to Early Devonian rocks in the Huntley Quadrangle, south-western Tasmania. Papers and Proceedings of the Royal Society of Tasmania 113: 5-13.

CASTER, K.E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology 34: 1-47.

1956. A Devonian placocystoid echinoderm from Paraná, Brazil. Paleontologia do Paraná (Centennial Volume): 137-148.

1983. A new Silurian carpoid echinoderm from Tasmania and a revision of the Allanicytidiidae. Alcheringa 7: 321-335

CASTER, K.E. & GILL, E.D. 1967. Family Allanicytidiidae, new family. Pp. 561-564. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas Press: New York).

GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology 41: 5-71.

HAUDE, R. 1995. Echinodermen aus dem Unter-Devon der argentinischen Präkordillere. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 197: 37-86.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3: 1-128.

JEFFERIES, R.P.S. 1984. Locomotion, shape, ornament and external ontogeny in some mitrate calcichordates. Journal of Vertebrate Paleontology 4: 292-319.

JEFFERIES, R.P.S. & LEWIS, D.N. 1978. The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. Philosophical Transactions of the Royal Society of London, Series B 282: 205-323.

KOLATA, D.R. & GUENSBURG, T.E. 1979. *Diamphidiocystis*, a new mitrate carpoid from the Cincinnatian (Upper Ordovician) Maquoketa Group in southern Illinois. Journal of Paleontology 53: 1121-1135.

KOLATA, D.R. & JOLLIE, M. 1982. Anomalocystitid mitrates (Stylophora, Echinodermata) from the Champlainian (Middle Ordovician) Guttenberg Formation of the Upper Mississippi Valley region. Journal of Paleontology 56: 531-565.

KONINCK, M.L. De 1869. Sur quelques échinodermes remarquables des terrains paléozoiques. Bulletin de l'Academie Royale des Sciences Belgique 28: 544-552.

PARSLEY, R.L. 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). Bulletins of American Paleontology 100: 5-57.

PHILIP, G.M. 1981. *Notocarpos garratti* gen. et sp. nov., a new Silurian mitrate carpoid from Victoria. Alcheringa 5: 29-38.

RUTA, M. (in press). A cladistic analysis of the anomalocystitid mitrates. The Zoological Journal of the Linnean Society.

RUTA, M. & JELL, P.A. 1999a. *Protocytidium* gen. nov., a new anomalocystitid mitrate from the Victorian latest Ordovician and evolution of the Allanicytidiidae. Memoirs of the Queensland Museum 43: 353-376.

1999b. *Adoketocarpus* gen. nov., a mitrate from the Ludlovian Kilmore Siltstone and Lochkovian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 377-398.

1999c. Two new anomalocystitid mitrates from the Lower Devonian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 399-422.

RUTA, M. & THERON, J.N. 1997. Two Devonian mitrates from South Africa. Palaeontology 40: 201-243.

UBAGHS, G. 1967. Stylophora. Pp. 496-565. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York ).

1969. Les échinodermes carpoides de l'Ordovicien inférieur de la Montagne Noire (France). Cahiers de Paléontologie (Editions du Centre National de la Recherche Scientifique: Paris) 1-112.

WILLIAMS, G.E. 1964. The geology of the Kinglake district, central Victoria. Proceedings of the Royal Society of Victoria 77: 273-328.

***DITHYROCARIS PRAECOX* IS A CARPOID.** *Memoirs of the Queensland* Museum *43(1): 452. 1999*:- Chapman (1904) erected *Dithyrocaris praecox* for a specimen 15mm long from fine siltstone of the Upper Silurian Melbourne Formation in Merri Creek, at Craigieburn just E of the Hume Highway, about 25km N of Melbourne (Sections 2 & 3, Parish of Kalkallo, Geological Survey of Victoria Sheet Bb3). *Dithyrocaris*, based on its type species, (*D. testudineus* (Scouler, 1835) from the Lower Carboniferous of Scotland, belongs to the primitive crustacean group Phyllocarida (Rolfe, 1969: 321, fig.147). Chapman's species does not belong to the Phyllocarida because the surface exposed is multiplated and thus the animal could not have been enclosed by a single piece carapace as in the Phyllocarida. Rather, *praecox* is a mitrate carpoid of the Family Allanicytidiidae. The plating arrangement (Fig. 1B) shows that the specimen represents the plano-concave surface of *Notocarpos* and because the anomalocystid plate C is on the right instead of the left (as normal in external view) it is an internal mould. Identifying *Notocarpos* are the wedge-shaped lateral orifice plates (not recognised by Philip (1981) but clear from his figs 4B, 5D, 6D), shape of the proximal lateral plates, proximal median plates and large central plate. While this specimen has no major features separating it from *Notocarpos garratti* Philip, 1981 and seems likely to belong to that species, seniority of its name would destabilise a widely used species name and provide a wholly unsuitable holotype as basis for the type species. I advocate isolation of the name *praecox* on the type specimen separating it from *garratti* by its smaller plate C and subquadrate body outline, thus preserving *garratti* as the type of *Notocarpos* and the widely used concept of the genus based on Philip's material and that presented by Ruta & Jell (1999).

**Literature cited**


CHAPMAN, F. 1904. New or little known Victorian fossils in the National Museum, Melbourne. Part 4. -Some Silurian Ostracoda and Phyllocarida. Proceedings of the Royal Society of Victoria 17: 298-319.

PHILIP, G.M. 1981. *Notocarpos garratti* gen. et sp. nov., a new Silurian mitrate carpoid from Victoria. Alcheringa 5: 29-38.

ROLFE, W.D.I. 1969. Phyllocarida. Pp. R296-R331. In Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part R. Arthropoda 4, vol. 1 (Geological Society of America & University of Kansas: Boulder, Colorado & Lawrence, Kansas).

RUTA, M. & JELL, P.A. 1999. Revision of Silurian and Devonian Allanicytidiidae (Anomalocystitida: Mitrata) from southeastern Australia, Tasmania and New Zealand. Memoirs of the Queensland Museum 43: 431-451.


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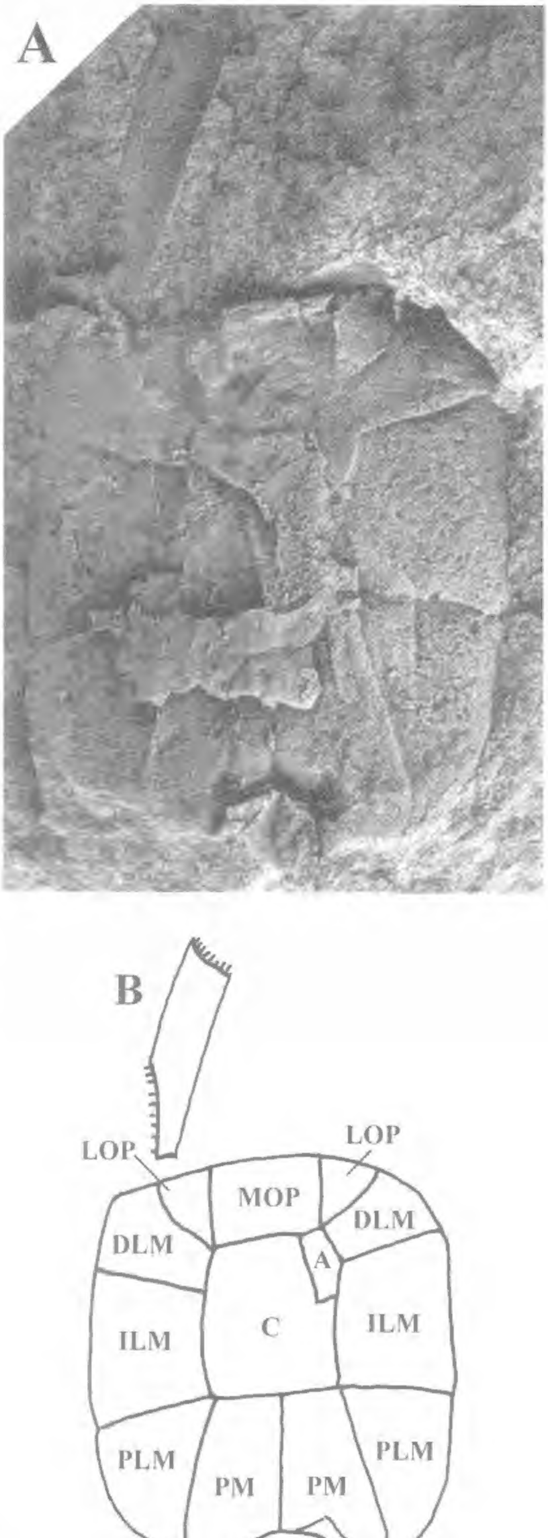


FIG. 1. *Notocarpos praecox* (Chapman, 1904). A, latex cast of the plano-concave surface of the internal mould of Museum of Victoria specimen NMVP4662, ×4. B, plating arrangement of plano-concave surface drawn from A.

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